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THE UNIVERSITY OF ALBERTA

THE REPRODUCTIVE BIOLOGY OF THE POLAR BEAR: A LARGE, SOLITARY CARNIVOROUS MAMMAL

by

©

MALCOLM ALEXANDER RAMSAY

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL 1986

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"The layman may wonder why a biologist is content to devote 50 years of his life to the study of bees and minnows without ever branching out into research on, say, elephants, or at any rate the lice of elephants or the fleas of moles. The answer to any such question must be that every single species of the animal kingdom challenges us with all, or nearly all, the mysteries of life. Working on minnows in winter and bees in summer I have not so far run out of problems to investigate. By deliberately restricting ourselves to very few carefully chosen experimental animals we end up by knowing our subjects very well indeed. Without this familiarity we should not be in a position to interpret their behaviour under experimental conditions...." *

---

*Frisch, Karl von. 1967. A biologist remembers. London: Pergamon Press

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE REPRODUCTIVE BIOLOGY OF THE POLAR BEAR: A LARGE, SOLITARY CARNIVOROUS MAMMAL submitted by MALCOLM ALEXANDER RAMSAY in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Date July 24, 1986

Abstract

Polar bears (*Ursus maritimus* Phipps) have a boreal, circumpolar distribution which approximates the extent of the sea ice in winter. I studied the population of polar bears inhabiting western Hudson Bay, near the southern extent of their range, during spring, summer, and autumn field seasons in 1981 through 1984. I determined population life-history parameters related to reproduction. Free-ranging bears were live captured in each season to obtain information on age-specific mean litter size, interbirth interval, age of first reproduction, reproductive senescence, cub survival, fidelity to maternity den sites, injuries sustained in mating activities and seasonal changes in body morphology. Whenever possible, these population parameters were compared with those from more northern populations of polar bears.

The long-term effects of chemical immobilization and handling on body weight, reproductive effort, cub survival, and movements on land were determined for 2,246 bears, older than one year, who were handled on 2,899 occasions. For most bears, the long-term effects associated with capture were apparently negligible in a time frame of months or years.

Most female polar bears conceive for the first time at 4 or 5 years of age. Reproductive senescence occurs in females older than 20 years. In the western Hudson Bay population, the natality rate for females in the 5 - 20 year age class was 0.86, 37% - 50% higher than that determined for any other polar bear population. Mean litter size in spring increased with age of female and approximately 20% of all females, 13 - 20 years of age, had litters of 3. About 40% of adult females had 2 year interbirth intervals, and 55% of cubs in their second year were independent of their mother. In populations at higher latitudes in Canada, triplet litters are rare (<1%) or absent, interbirth intervals of 2 years are uncommon, and few cubs are weaned in their second year.

I propose that the dynamics of sea ice and the associated unpredictability in access to food have played a major role in the evolution of the social structure and mating system of polar bears. Adult males and females must move to areas of the sea ice where prey are available. The locations of these regions, however, can be both

seasonally and annually unpredictable. This, in turn, makes female distributions unpredictable. Therefore, adult males are unable to defend stable territories that encompass the home ranges of one or more females. Instead they distribute themselves among different sea ice habitats at the same relative densities as solitary adult females. Male dominance hierarchies are unstable and evidence of intense fighting during the breeding season is common.

Polar bears may be adapted to survive longer fasts than any other mammal. Energy needs during fasting appear to be met by metabolism of fat and nitrogenous wastes recycled to meet protein requirements. The intermediate metabolic pathways adopted during long-term fasting appear to be similar to those used by all Holarctic bears while hibernating. Polar bears may, however, be able to switch facultatively into this protein conserving metabolic state in response to food availability and without regard to season.

Bears give birth to tiny, immature young that are significantly smaller than predicted for the size of the mother. I propose that this reflects a physiological constraint on the ability of a pregnant female to meet the requirements of fetal metabolism while in a state of winter dormancy and without access to food or water. By shortening the period of gestation and giving birth to very small, immature neonates, a female bear can shift from transplacental to mammary nourishment of her offspring. This allows fatty acids from maternal lipid stores to be used directly for nourishing her offspring, thereby sparing her body protein from use in gluconeogenic pathways.

Mammals in a patchy environment are often required to make regular spatial movements to obtain necessary resources. I describe the routes followed by adult female polar bears in spring from their winter dens to the sea ice of Hudson Bay where they hunt. Tracks made by adult females accompanied by cubs-of-the-year followed markedly straight and relatively parallel courses toward the sea. The remaining tracks, made by solitary adult females, followed a similar heading but along more convoluted routes. Neither group took the mean heading of the shortest route to the sea.

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One of the great tragedies of our modern world is that little time is available to most people to consider the world about them. I was extremely fortunate to be offered the luxury of both the time and resources to indulge in such a delightful pastime. I am grateful to the Canadian National Sportsmen's Association, The Isaac Walton Killam Fund, the Max and Marjorie Ward Fund, and the University of Alberta for the personal support that allowed me the time to carry out my research program and to think about the patterns I saw.

I had the honour to work with two fine scientists as my research co-supervisors; Drs. Jan Murie and Ian Stirling. Each inspired me, by their example, to appreciate the beauty of tightly reasoned scientific enquiry. The excitement that one can experience from a scientific research program can be wildly exhilarating. Both Jan and Ian were patient enough to not discourage my joy and yet were able to force me to sharpen my critical faculties. I would also like to pay tribute to my other supervisory committee members, Drs. Robert Hudson and Fred Zwickel, who gave valuable criticism of my ideas.

It would be impossible to thank all of the people who have assisted me during the course of my studies. Nonetheless, I would like to at least list those who particularly stand out in my mind and who contributed much to the enjoyment I realized during my research program.

Wendy Calvert, Holly Cleator, Jim Hines, Michael Kingsley, Jan Murie, Ralph Nelson, and Ian Stirling read early drafts of some or all of the chapters and offered much constructive criticism. Michael Kingsley also offered statistical advice and Wendy Calvert assisted me in numerous ways and patiently showed me the value of rigorous work in the laboratory; I hope I have not been too trying for either.

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1. INTRODUCTION

Even before I initiated my studies I was intrigued by some of the novel ecological, behavioural, and physiological adaptations that have enabled polar bears (*Ursus maritimus*) to be so successful in what superficially appeared a rather inhospitable environment. I proposed to carry out a first-order descriptive natural history of the reproductive biology of polar bears with the intention that this framework would enable me to develop meaningful insight into some of their adaptations. I was especially interested in how such adaptations might constrain and modify aspects of the bears' reproductive biology.

It is frequently the case in science that basic research not only increases our understanding of the dynamics of the natural world but it can supply the foundation from which applied sciences can be developed. Today much basic ecological research is urgently needed if wise conservation practices are to be developed for the preservation of many species of plants and animals. When I began my research, concern was being expressed that some polar bear populations in Canada might have experienced excessive pressure from hunting by Inuit and that some might soon be adversely influenced by industrial activities in the Arctic. Basic data on reproductive parameters were either lacking or insufficient to adequately address managerial decisions stemming from these concerns. My studies should provide some of the parameters necessary to assess the dynamics of at least one population in the Canadian Arctic.

Bears (Ursidae) are prominent members of the mammalian fauna wherever they are found and include the largest of the Carnivora as well as some of the largest terrestrial mammals (Nowak and Paradiso 1983). They are or were found on all continents except Australia and Antarctica. Yet in spite of their conspicuousness and ubiquity, many details of their reproductive biology are incompletely known. Questions relating to changes in reproductive parameters with age and concomitant effects on lifetime reproductive success, effects of environmental perturbations on subsequent reproductive effort, energetic costs of reproduction, and strategies of energy accumulation and storage relative to reproductive effort, the degree of natal philopatry, and den site fidelity are, at best, only partly answered. Similarly, little is known of behaviour associated with mating and other reproductive activities.

As would be expected for a large, long-lived organism (Calder 1984), bears display low reproductive rates, amongst the lowest recorded for terrestrial mammals. As a consequence, they are slow to recover from population reductions. Three major factors influence reproductive rates: litter size, age of first reproduction, and interbirth interval (Knight and Eberhardt 1985). Although litters are not markedly smaller than would be expected for animals of their size, bears breed for the first time at a relatively late age and the interval between successive births is relatively long (Bunnell and Tait 1981). The long interbirth interval is proximally mediated by a long period of association with cubs. The presence of unweaned young appears to inhibit oestrus and the initiation of a new reproductive cycle (Baker 1912, Erickson and Nellor 1964, LeCount 1983). Entire populations of bears are also known to experience complete or partial reproductive failure in years when food resources are significantly reduced (Jonkel and Cowan 1971, Martinka 1974, Rogers 1976, Stirling et al. 1976, Picton 1978). The availability and abundance of food resources appear to exert a strong effect on realized reproductive rates for all species of bears for which data are available.

An organism rarely exists in stasis, and flux of energy and resources through metabolic pathways is characteristic of life itself (Maynard Smith 1986). All mammals follow a characteristic time-sequence of major developmental stages throughout their lives (Fig. 1-1). The relative length of time spent in each stage is a characteristic available for modification by both mother and offspring (Dunbar 1982). Presumably, selection occurs for developmental rates that result in the greatest propagation of the genotype. Although bears follow the same basic developmental sequences as other mammals, they display a number of modifications that are anomalous enough to be worthy of note.

Mating occurs in the spring for all species of Holarctic bears (brown, *U. arctos*; black, *U. americanus*; and polar), but implantation of blastocysts is delayed until autumn (Wimsatt 1963, Asdell 1964, Hensel et al. 1969, Lønø 1970, 1972). At about the time of implantation, females cease feeding and enter dens in which they spend the winter without food and water. The length of time spent in an overwinter den varies among populations of both brown and black bears, generally being longer with increasing latitude (Johnson and Pelton 1980). Gestation and early post-partum lactation occur while the mother is fasting. No other mammals, except some of the large mysticete cetaceans, go without food and water for extensive periods during active gestation (Frazer and Huggett 1973). Similarly, only bears, some cetaceans, and some phocid pinnipeds fast through part or all of the lactation period (Fedak and Anderson 1982, Lockyer 1981). The period of gestation is markedly short for bears and cubs are born in an immature state, significantly smaller relative to their mother than predicted for eutherian neonates (Leitch et al. 1959, Frazer and Huggett 1974, McKeown et al. 1976). The period of lactation is correspondingly longer with extended postnatal bonding. The pattern of relatively short foetal development and relatively extended lactation is more characteristic of a metatherian reproductive strategy than that of a eutherian (Renfree 1983, Lee and Cockburn 1985). After weaning, young bears are independent for one or more years before they reach reproductive maturity, a time during which they attain considerable somatic growth.

Although most bears have secondarily adopted an omnivorous or herbivorous diet, polar bears, recently evolved from brown bear ancestors (Erdbrink 1953, Kurten 1964), have reverted to a largely carnivorous feeding mode (Hylander 1978), preying primarily on ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*). Polar bears have also evolved to live on the sea ice of the Arctic Ocean, an environment qualitatively different from the terrestrial habitats exploited by other bears. One of the most significant environmental differences experienced by polar bears results from the labile nature of sea ice which leads to spatial and temporal variability in access to resources, primarily seals and mates (Stirling and McEwan 1975, Smith and Stirling 1978, Smith 1980). Although long-term average sea-ice conditions and productivity are generally predictable, local conditions may vary significantly both within and among seasons (Jacobs and Newell 1979, Catchpole and Faurer 1983). Polar bears are therefore obliged repeatedly to search out anew, areas of sea ice habitat where seals are abundant and accessible. In some years this may entail movements of considerable distance (Schweinsburg et al. 1982, Lentfer 1983). Consequently, neither male nor female bears maintain discrete home ranges as do black and brown bears (Amstrup and Beecham

1976, Young and Ruff 1982, Servheen 1983). Bears are generally considered solitary mammals with the family group, mother and accompanying cubs from her last parturition, being the only stable social unit (Herrero 1979). At particularly rich feeding areas bears may congregate and show tolerance of conspecifics (Craighead et al. 1969). The absence of discrete home ranges and defended territories among polar bears may result in behavioural differences from other bears with adults occasionally displaying intraspecific tolerance and even non-agonistic interactions during times of both extreme food abundance and when food is scarce (Latour 1981, Hansson and Thomassen 1983, Lunn and Stirling 1985).

Whereas all members of terrestrial bear populations enter overwinter dens each autumn, only pregnant polar bears do so. All other age and sex classes remain active all winter, constructing temporary dens only during periods of inclement weather (Harington 1968, Lønø 1970). Presumably this reflects differences in the overwinter availability of food for ice-living versus terrestrial bears. In most populations of polar bears, pregnant females inhabit maternity dens that are constructed on land. In some regions the maternity dens are clustered in restricted areas, resulting in relatively high local densities of active dens (Harington 1968, Jonkel et al. 1972, Uspenski and Kistchinski 1972, Hansson and Thomassen 1983). In other populations, maternity dens are widely distributed at relatively low densities or even constructed in snow drifts on the sea ice (Lentfer 1975). Reasons for between-population differences in the degree of gregariousness at den sites or in the habitat chosen for dens are not clear but may reflect the distribution of suitable habitat for dens. At present the specific requirements for den sites are only partially understood.

Terrestrial bears enter overwinter dens soon after their annual peak period of feeding. The equivalent nutritional state for polar bears, however, is in the late spring and early summer (Smith 1980), well before the time of autumn den entry. In some populations, like those inhabiting Hudson and James Bays, all the sea ice melts each summer and bears lose access to seals. Consequently, female polar bears there may begin fasting and losing weight several months before entering dens (Lunn and Stirling 1985). In populations where access to prey may be limited during summer, bears of all age and sex classes may seek out or construct temporary dens and resting sites where they can await the resumption of hunting opportunities, presumably while minimizing energetic costs (Doutt 1967, Stirling et al. 1977, Knudsen 1978, Schweinsburg 1979, Latour 1981).

The results of my investigations are presented as a series of manuscripts, each addressing some facet of polar bear natural history, with particular emphasis on aspects of their reproduction.

First, in Chapter 2, I examine the long-term effects of capturing free-ranging polar bears. Although effects of capture are presumed to be negligible in most live-capture field studies, measures of induced biases are seldom reported. The validity of much of my work depends on there being little bias introduced from the handling methods. Therefore, I consider the analysis presented in Chapter 2 to be a critical underpinning for the rest of my thesis.

Chapter 3 summarizes reproductive parameters for the population of polar bears inhabiting western Hudson Bay with comparison made, when possible, to other populations. Animals were sampled using live capture to determine such basic parameters as mean litter size, interbirth interval, age of first reproduction, reproductive senescence, and cub survival. Serum progesterone levels were determined for females at several stages in their reproductive cycle to provide corroborative support for the models generated from the capture data. Tenure at and fidelity to den sites were also investigated because of the influence they may have on other aspects of reproduction in polar bears.

The breeding system of polar bears is described in Chapter 4, deduced principally from indirect evidence. It is compared to the breeding systems of other species of bears.

Some implications of the feast-fat cycle of polar bears are investigated in Chapter 5. Serum urea and serum creatinine levels were determined for free-ranging individuals during the period when they were on land in northeastern Manitoba. These blood constituents serve as markers to indicate the metabolic state adopted by black bears when feeding or during their overwinter fast. The marked differences between polar and terrestrial bears in their feeding and activity patterns suggested that examination of polar bear blood constituents might offer insight into the range of their metabolic adaptations to life on polar sea ice.

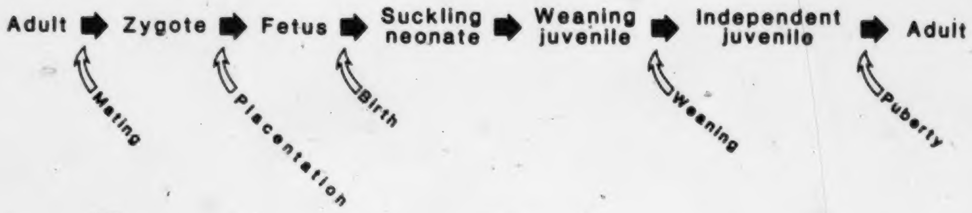
In Chapter 6 the question of the anomalously short gestation period and correspondingly tiny size of cubs at birth is addressed. The physiological model proposed to account for this anomaly may have wider implications both for bears and for life-history theory of mammals in general.

Finally, Chapter 7 describes the routes taken by polar bear family groups in spring as they leave the inland maternity denning region in northeastern Manitoba and move to the sea ice of Hudson Bay. Polar bears must often move long distances to find necessary resources. That polar bears can make directed movements to particular regions in different seasons has been assumed, but has never before been demonstrated.

Figure 1-1. Schematic representation of some major developmental phases occurring in the life time of a typical mammal (after Hochachka and Somero 1984).

➡ indicate time sequence

⇧ represent events of particular significance in the life of a mammal.


Adult
Zygote
Fetus
Suckling neonate
Weaning juvenile
Independent juvenile
Adult
Mating
Placentation
Birth
Weaning
Puberty

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2. LONG-TERM EFFECTS OF DRUGGING AND HANDLING FREE-RANGING POLAR BEARS[1]

2.1 Introduction

In long-term studies of the ecology and behaviour of wildlife, it is often necessary to identify individual animals. Some species may be individually identified without handling and marking (Pennycuick 1978); however, for many others and for certain procedures; e.g., weighing, tissue sampling, marking, and attaching radio-transmitters, individuals must usually be handled. A variety of techniques for capturing and handling free-ranging animals has become commonplace in wildlife investigations (Day et al. 1980).

An assumption frequently made when handling and marking wild animals is that survival, behaviour, or fitness is not affected (Lehner 1979, Seber 1973). This assumption is not often verified, especially over relatively long time periods. Some short-term physiological changes associated with capture and handling have been described for polar bears (*Ursus maritimus*) (Lee et al. 1977). Seal et al. (1970) reported no fetal losses or miscarriages in any of the 3 North American bear species when 6 captive animals were immobilized 19 times with phencyclidine hydrochloride during pregnancy. Craighead et al. (1976) concluded that chemical immobilization and handling of brown bears (*U. arctos*) had no substantial effect on subsequent reproductive rates. Amstrup and Beecham (1976) concluded the activities of investigators had a negligible effect on American black bears (*U. americanus*). However, Miller and Ballard (1982) suggest that handling and relocating brown bears did lead to higher-than-normal mortality of young and lower-than-normal productivity for adult females. Den abandonment and, in some cases, weight loss have been reported for denning bears disturbed by the activities of investigators (Craighead and Craighead 1972, Belikov 1976, Reynolds et al. 1976, Hamilton and Marchinton 1980, Tietje and Ruff 1980, Alt and Gruttadauria 1984).

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Although I do not know, *a priori*, how long-term deleterious effects of handling polar bears might be manifested, I hypothesized that recaptured bears might show, on average, some combination of reduced body weights, smaller litter sizes, lower cub survival rates, changes in behaviour, or shifts in home range. To test these hypotheses, I compared data collected from polar bears in Canada at the time of their 1st capture to those from bears recaptured ≥2 months after their initial capture.

2.2 Study area

In the Canadian Arctic immobilizing and tagging polar bears began in 1966 and has continued to the present. I include data from bears handled between 1967 and 1984, inclusive, from western Hudson Bay, the eastern Canadian Arctic, the high and low central Canadian Arctic archipelago, and the eastern portion of the Beaufort Sea. These regions approximate the limits of discrete populations of polar bears as determined by mark-recapture studies (e.g., Stirling et al. 1977, Stirling et al. 1980, Furnell and Schweinsburg 1984, Amstrup et al. 1986). Many people have participated in the tagging operations, and handling procedures varied between individuals and through time. As of August 1984, 2,246 individual bears ≥1 year old had been drugged and handled on 2,899 occasions, with a minimum interval between recaptures of 2 months. The proportion of recaptured bears, in each season, ranged between 0.19 and 0.30.

2.3 Methods

Most polar bears in the Canadian Arctic were captured from a helicopter by shooting with projectile syringes filled with an immobilizing drug using standard Cap-chur equipment (Palmer Chemical Co., Douglasville, Ga.) (Lentfer 1968, Larsen

1971). In western Hudson Bay culvert traps, Aldrich leg snares, and darting of free-ranging bears from the ground also have been used for capture of a small number of bears (Stirling et al. 1977). The drugs succinylcholine chloride (Anectine) or phencyclidine hydrochloride (Sernylan) mixed with promazine hydrochloride (Sparine) were used for immobilization prior to 1970 (Lentfer 1968). Since 1970, almost all immobilized bears have received either Sernylan with Sparine or a 1:1 mixture of ketamine hydrochloride (Ketaset) and xylazine hydrochloride (Rompun) (Lee et al. 1981). Carfentanil, etorphine hydrochloride, and tiletamine hydrochloride mixed with zolazepan hydrochloride (Telezol) have been used experimentally since 1979, but on fewer than 200 bears (Haigh et al. 1983, 1985, Stirling et al. 1985).

Since 1980, a prophylactic dose of penicillin was administered to all bears handled. Animals immobilized with Ketaset and Rompun temporarily lose the blink response so that their eyes remain open. Consequently, ophthalmic ointment was applied to the eyes, and they were covered with soft reinforced paper towelling to prevent the surface of the eye from drying, to keep out foreign objects, and, in summer, to protect them from biting insects. An antibiotic cream (Hibitane) was applied to the dart wounds. Bears were turned to face away from the wind after handling, and cubs were placed on the leeward sides of their mothers. During summer, rectal temperatures were monitored, and water was poured over the fur to avoid hyperthermia. In 1984, yohimbine was used as an antagonist for Ketaset and Rompun (Ramsay et al. 1985).

Once immobilized, bears were tagged on both ears, tattooed on each upper lip, measured, and had a premolar tooth extracted for age determination. In most instances temporary numbers were painted on the animals with black Nyanzol dye or hair dye to facilitate short-term identification from the air. Since 1982, blood samples were taken from most bears by femoral venipuncture.

Body weights of bears $\geq$1-year old were determined by measuring axillary girth and calculating body weight using the close relationship ($r = 0.97$) between scale weight and axillary girth (Stirling et al. 1977). In spring, cubs-of-the-year, 2-4 months of age, were weighed using spring scales.

Male polar bears are larger than females (Kingsley 1979), and weight differences between male and female cubs-of-the-year are apparent by approximately 9 months of age. Polar bears of all ages also display marked seasonal variation in body weight with a maximum reached in early summer and a minimum in late winter. Accordingly, I categorized data on body weights of bears $\geq$1 year old by sex, age, capture status, and season. Females were subdivided further as being with cubs or solitary. The age classes used were yearlings, 2-year-olds, subadults (3-4 years old for females or 3-6 years old for males), and adults ($\geq$5 years old for females or $\geq$7 years old for males). Cubs-of-the-year were omitted from the analysis on the effect of handling on body weight because few were recaptured during their 1st year of life. Bears were separated into 2 categories, bears not previously handled (1st-captures) and those handled at least once previously (recaptures). The seasonal categories used were winter-spring (February - May), summer (June - August), and autumn (September - November). No bears were handled in December and January. Data from bears handled at or near the Churchill, Manitoba garbage dump were omitted from analyses on body weight because they were known to gain weight and to be heavier than other bears during the same season (Lunn and Stirling 1985). Many bears using the dump also showed a high degree of seasonal fidelity, and each had been handled on several occasions. Therefore, their inclusion in analyses would tend to bias mean weights of recaptured bears.

I examined the effect of handling on body weight using forward-selection stepwise multiple linear regression (Sokal and Rohlf 1981). A common logarithm transformation of body weight was used to approximate homogeneity of variances between samples. These transformed data were used as the dependent variable, and binary dummy variables were created for age-class, season, capture status, and, for adult females, reproductive status (Snedecor and Cochran 1980). Each variable was allowed to enter the stepwise regression equation if the square of its multiple correlation with variables already in the equation was < 0.95. The logarithm of body weight was regressed on the binaries for age, season, and reproductive status; a test for the effect of handling on body weight then was obtained by allowing the variable for recapture status to enter the regression equation and observing whether the correlation coefficient was significantly improved. Because different age-class groupings were assigned to males and females and because females were subdivided by whether they had accompanying cubs, the sexes were considered separately in the regression analyses. Comparison between the logarithm of mean weight for first-captured vs. recaptured bears, by season, age, and reproductive category, were made using pairwise multiple *t*-tests. Bonferroni levels of significance were used to test for differences between paired sample means (Games 1971).

I compared the effects of capture of females on the sizes of their litters during subsequent recaptures using 2-way analysis of variance modified for unequal sample sizes. Individual cub weights in spring were, on average, greatest for single cubs and least for triplets. Accordingly, an analysis of covariance, with litter size as the covariate, was used to determine the effect of capture status on cub weight (Sokal and Rohlf 1981).

I recognize the weakness that these tests do not account for length of interval between captures. Presumably, any handling effect will have the greatest impact soon after handling and increasingly lower magnitude as time passes. I did not incorporate any measure of age of 1st capture in the tests. The long-term effects of handling might be different for a bear 1st handled as a cub or subadult rather than as an adult. Finally, I have no measure of the number of bears that disappeared from a studied population as a result of handling.

All statistical calculations used MIDAS (Statistical Research Laboratory, The University of Michigan) or BMDP (Department of Biomathematics, The University of

California, Los Angeles) statistical software.

2.4 Results

2.4.1 Body weight

For all age-class divisions and for both 1st-captured and recaptured bears, mean weights were greatest in summer, at or soon after a period of hyperphagia (Tables 2-1 and 2-2).

For males, 5 variables for age and season explained 71% of the total variance in body weight (F = 551, $P << 0.001$), none of the others significantly improved the estimate. The inclusion of recapture status also failed to improve the estimate ($P = 0.48$), and the R^2 value increased only 0.01% (Table 2-3). Mean weights of recaptured males therefore, were not significantly lower, by season, for any age class. The only age and season class with a significant difference in weight based on capture status was 2-year-old males in summer, when recaptured animals were significantly heavier than those caught for the 1st time (Table 2-1, $t_s = -3.85$, Bonferroni $P < 0.05$).

Stepwise linear multiple regression on the logarithm of body weight for female bears determined 6 variables that collectively explained 63% of the variance in body weight (F = 373, $P << 0.001$). When recapture status of the bears was entered into the regression a small (0.27%) but significant ($P = 0.023$) improvement in predictive value resulted (Table 2-4). The negative correlation coefficient associated with recapture status in the regression indicated that recaptured females were, on average, lighter in weight than females on their 1st capture. Over all seasons, the only consistent trend in weight relations for any age and reproductive class was for adult females with cubs which tended to be lighter than 1st-captured female bears with cubs (Table 2-2). Despite this trend, females with cubs in winter-spring was the only subset of the female sample that differed in weight by capture status; bears on their 1st capture were significantly heavier than recaptured bears ($t = 3.01$; Bonferroni $P < 0.05$). No trends were apparent in any other age or reproductive class of females, suggesting that any negative effects of handling on the body weights were among females with cubs.

2.4.2 Litter Size

Mean size of litters varied significantly between age classes of cubs but did not vary significantly for cubs of recaptured mothers vs. cubs of mothers not previously handled (Table 2-5) (capture status $F = 1.48$, $P = 0.2$; age of cubs $F = 12.5$, $P << 0.001$; interaction $F = 0.5$, $P = 0.6$). Nonetheless, for all three cub age-classes, the mean litter sizes of recaptured females consistently tended to be lower than for mothers not previously handled. No measure was made of the number of captured females that subsequently lost whole litters prior to weaning as it was not possible to obtain a comparative measure of litter loss from bears not handled. However, if handled females tended to lose whole litters more frequently than those not handled there would be a greater separation in the mean litter sizes by capture status than that shown in Table 2-5.

2.4.3 Spring Weight of Cubs-of-the-Year

Cubs are born in snow dens and do not emerge until early spring at approximately 2-3 months of age (Harington 1968, Lønø/ 1970). In northern Manitoba polar bears den overwinter >10 km inland from the sea ice (Stirling et al. 1977). By capturing family groups there in spring, I was able to obtain weights of cubs that had emerged from their dens prior to their mothers' feeding on seals (Table 2-6). Mean weights of cubs varied significantly between litters of different sizes ($F = 59.70$; $P < 0.0001$) but were not different for cubs of mothers of different capture status ($F = 1.48$; $P = 0.2$). Nonetheless, for each litter size, the mean weight of cubs of mothers previously handled consistently tended to be slightly lower than that of mothers not previously handled.

2.4.4 Pregnant Females at Den Sites

Thirteen bears found in dens and thought to be pregnant, were handled in autumn (Oct-Nov) between 1980 and 1984 and were resighted at least once more in the autumn of capture or were recaptured or resighted at dens in the spring (Feb-Mar) following capture. Three of the bears re-entered their den, or a den ≤ 2 km from their initial den, soon after recovery. The other 10 bears moved away from their capture sites. The median distance moved was 14.0 km ($\bar{X}$ distance = 17.8 km; range = 0-60 km). I have no comparative data on the frequency of spontaneous den abandonment by pregnant females in autumn that had not been disturbed by human activity.

2.4.5 Adult Males in Autumn

In western Hudson Bay polar bears are forced ashore in late-summer and autumn when the sea ice melts. Most adult males then are found on land along Hudson Bay (Stirling et al. 1977) where little food is available. The bears are relatively sedentary then rather than actively foraging (Knudsen 1978, Latour 1981, Lunn and Stirling 1985). When ice re-forms in late autumn they move back onto Hudson Bay. Unlike pregnant females that fast all winter and live off their body stores, adult male polar bears do not hibernate. Pregnant females presumably also have relatively greater metabolic demands than do adult males (Freinkel et al. 1972). This may result in males in autumn having fewer energetic constraints to moving when disturbed than do pregnant females. Yet, 37% of 32 adult males were resighted, in the same autumn season, ≤ 2 km from their location of capture. The median distance moved by all males was 2.7 km ($\bar{X}$ distance = 10.5 km, range = 0-45.2 km). There was no significant difference between pregnant females and adult males in the median distance moved (Mann-Whitney U = 253.5; P = 0.25; n = 45), or in the proportion that moved after capture (G^2 = 0.90; df = 1; P

> 0.34). Nonetheless, of the bears that did move >2 km, pregnant females moved a median distance almost twice that of males (24.5 km for females vs. 12.3 km for males).

2.5 Discussion

The null hypothesis that handling of polar bears has had no significant long-term effects could not be rejected in most of the categories tested. However, there were enough indications of negative correlations between handling and some parameters to warrant note, although the differences were not statistically significant. The consistency of trends suggests that handling may have a slight long-term negative effect on some bears, especially on adult females with cubs. It is possible, but not demonstrated, that the stress of handling may cause females with cubs to move more often than non-handled bears or react more strongly to human produced stimuli such as the sounds of distant aircraft.

Bears displaying aberrant behaviors as a result of handling could have had higher energy expenditures or lower rates of food intake than bears that were not handled. For example, females handled in spring during the period of active feeding may have moved away from prime feeding areas and thus lowered their total food intake. Additional energy costs incurred after the annual peak period of feeding would have to be met from body stores, a potentially critical cost for pregnant females prior to overwinter hibernation. Because polar bears are inefficient walkers (Hurst et al. 1982), induced walking or running might result in significantly higher maintenance costs and a concomitant reduction in the amount of body stores available for over-winter maintenance and cub production. Finally, the weights of cubs in spring are directly correlated with their mother's weight during the preceding autumn (Rogers 1976, Chapter 3). Therefore, any energy costs to a pregnant female resulting from increased activity after being handled might result in a reduction in the weight or size of her litter the following spring. Smaller body size is associated with increased mortality in cubs (Rogers 1976, Chapter 3). The data are not adequate, however, to test these hypotheses nor to evaluate whether den abandonment in autumn has a negative influence on subsequent cub production. Further attention to monitoring the effects of handling on the reproductive success of pregnant females and females with cubs appears warranted.

In considering the effects of handling on adult females, however, I have adopted a conservative view and emphasized those cases where effects are most pronounced. In contrast, mean weights of yearling and subadult females, adult females without cubs, and males of all age classes were not significantly different nor did they show any consistent trends by capture status. The size of samples was, in most cases, large and the general absence of statistical significance between treatment means argues against biological significance resulting from handling, at least in the parameters measured. The negative partial correlation of female body weight with previous handling (Table 2-4) may be spurious and may not reflect causality. Females may put more stored resources into reproductive effort with increasing age, as has been proposed for some other vertebrate species (Charlesworth 1980). As recaptured bears were, on average, older that first-captured bears, differences between them in body weight might reflect changing life history strategies with age (Chapter 3). Data currently are lacking to test this hypothesis.

At present I do not know the full biological significance of the observed effects of handling female polar bears. However, I conclude that they are acceptably small. Certainly, they do not appear to perturb polar bears to the point of severely biasing data.

Table 2-1. Seasonal mean whole body weights (kg) for male polar bears in the Canadian Arctic (1967-1984) by season, age class, and capture status.

		Winter-spring (Feb-May)			Summer (Jun-Aug)			Autumn (Sep-Nov)		
Age class	Capture status	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
Yearling	1st capture	71.2	2.3	52	128.8	7.5	20	113.2	3.9	38
	recapture	71.3	7.9	8	126.0	30.4	3	118.6	11.2	5
2-year-old	1st capture	121.5	4.6	66	155.1 α	7.7	23	145.7	5.0	33
	recapture	140.6	9.7	7	195.0 α	8.4	5	142.6	8.1	12
Subadult	1st capture	220.8	4.5	267	256.0	9.7	62	221.5	7.8	60
	recapture	223.1	9.4	48	255.6	8.2	26	218.3	7.9	40
Adult	1st capture	355.4	5.3	283	382.6	12.2	72	335.5	8.2	62
	recapture	332.9	8.3	97	382.4	17.6	38	321.7	10.7	25

Total 1st capture	668	177	193
Total recapture	160	72	82

α - means of common logarithm of whole body weight differ (Bonferroni $P < 0.05$) between capture groups.

Table 2-2. Seasonal mean whole body weights (kg) for female polar bears in the Canadian Arctic (1967 - 1984) by season, age class, reproductive status, and capture status.

		Winter-spring (Feb-May)			Summer (Jun-Aug)			Autumn (Sep-Nov)		
Age class	Capture status	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
Yearling	1st capture	59.6	1.5	84	103.9	5.5	24	84.1	3.3	43
	recapture	52.0	3.0	4	123.0	9.9	4	85.8	11.5	6
2-year-old	1st capture	95.3	2.6	68	135.7	6.7	26	120.0	3.8	29
	recapture	76.9	4.6	9	135.9	11.7	8	121.8	15.7	6
Subadult	1st capture	139.1	2.5	158	168.6	10.8	28	171.8	7.2	38
	recapture	140.7	6.4	17	192.8	9.1	6	155.6	10.2	8
Adult with cubs	1st capture	162.7 α	1.9	316	195.5	4.5	65	164.3	5.0	46
	recapture	152.4 α	2.9	124	188.9	5.7	34	150.8	4.2	34

Adult alone	1st capture	162.5	2.6	206	249.4	11.6	49	237.3	10.9	24
	recapture	162.9	4.5	54	248.6	18.7	12	212.2	17.1	11
Total 1st capture				832			192			180
Total recapture				208			64			65

α - means of common logarithm of whole body weight differ (Bonferroni $P < 0.05$) between capture groups.

Table 2-3. Coefficients for multiple regression on log body weight for male polar bears.

Predictor variables	Partial correlation	Coefficient	SE	*t*	*P*
Intercept		4.433	0.026	169.74	<0.0001
Summer	0.230	0.182	0.021	8.68	<0.0001
Autumn	0.101	0.080	0.021	3.72	0.0002
2-year-old	0.302	0.395	0.039	11.64	<0.0001
Subadult	0.660	0.901	0.028	32.23	<0.0001
Adult	0.801	1.357	0.028	49.12	<0.0001
Recapture status	-0.019	-0.020	0.029	-0.71	0.48

Table 2-4. Coefficients for multiple regression on log body weight for female polar bears.

Predictor variables	Partial correlation	Coefficient	SE	*t*	*P*
Intercept		5.209	0.020	258.11	<0.0001
Spring	-0.433	-0.310	0.016	-18.85	<0.0001
Autumn	-0.147	-0.123	0.021	-5.83	<0.0001
Yearling	-0.633	-0.750	0.023	-32.02	<0.0001
2-year old	-0.347	-0.350	0.024	-14.51	<0.0001
Solitary adult	0.258	0.200	0.019	10.45	<0.0001
Adult with cub	-0.130	-0.080	0.016	-5.13	<0.0001
Recapture status	-0.058	-0.048	0.021	-2.27	0.023

Table 2-5. Mean size of cub-of-the-year, yearling cub, and 2-year-old cub litters in the Canadian Arctic, 1967-1984, by capture status of mother.

	1st capture			Recapture		
Age of cubs	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
Cub-of-the-year	1.74	0.03	267	1.73	0.05	178
Yearling cub	1.58	0.05	129	1.46	0.07	54
2-year-old cub	1.50	0.07	66	1.42	0.11	19
Total			462			251

Table 2-6. Mean body weights (kg) for cubs-of-the-year handled in February and March in N.E. Manitoba, 1980-1984, by capture status of mother and litter size.

	1st capture			Recapture		
Litter size	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
Single	14.4	1.1	16	13.9	2.0	7
Twin	11.3	0.3	86	10.9	0.3	66
Triplet	8.7	0.8	15	8.3	0.6	25
Total			117			98

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3. REPRODUCTIVE BIOLOGY AND ECOLOGY OF FEMALE POLAR BEARS

3.1 Introduction

A preliminary study indicated that the population of polar bears inhabiting western Hudson Bay differed in several reproductive parameters from other Canadian polar bear populations (Ramsay and Stirling 1982). Specifically, the mean litter size appeared larger, mean interbirth interval shorter, and overall natality rate higher in western Hudson Bay than in other populations studied. In this study I describe, using a larger sample size of bears and in greater detail than hitherto, the reproductive productivity of female polar bears from western Hudson Bay. A primary intent was to determine the reproductive characteristics of this population and to generate testable hypotheses to account for differences among populations. Because nutritional status appears to play a major role in regulating the reproductive performance of all species of bears (Jonkel and Cowan 1971, Martinka 1974, Rogers 1976, Stirling et al. 1976, Picton 1978), I paid particular attention to body weight as a possible indicator of nutritional condition. When possible, comparison of measured parameters was made between the bears of western Hudson Bay and those from more northern Canadian populations. Research was based primarily on field studies and samples of bears were captured each year over a six year period. In addition to being able to generate cross-sectional reproductive parameters for the population, I also obtained partial reproductive histories of some females, thus generating information on interbirth intervals, cub mortality, pregnancy rate, and fidelity to winter den sites.

The polar bears of western Hudson Bay were initially chosen for detailed study because the region contains the densest concentration of overwintering female bears known from Canada in a traditional denning area that has been known to have been active for at least 200 years (Hearne 1795). At the time I began this research, a large amount of information had already been collected for this population from various studies conducted over the preceding 15 years (Stirling et al. 1977). These data, although collected with different objectives than in the current study, provided baseline information to assist in planning studies, as well as comparative historical background information. Finally, field logistics from the town of Churchill, Manitoba are markedly less expensive than if conducting similar research at any other potential sites in the Canadian Arctic.

Preliminary descriptions of the reproductive life-history of females in the study population have been given by Stirling et al. (1977) and Ramsay and Stirling (1982). Aspects of the behaviour of females using the Manitoba denning region in winter and spring were described by Jonkel et al. (1972), Ramsay and Stirling (1984), and Ramsay and Andriashek (1986). Several studies have reported on some features of the reproductive biology of female polar bears in other populations, particularly those relating to population dynamics (e.g. Lønø 1970, Uspenski and Kistchinski 1972, Stirling et al. 1976, 1980, 1984, Lentfer et al. 1980, Hansson and Thomassen 1983, Furnell and Schweinsburg 1984, Larsen 1985).

3.2 Methods

3.2.1 Study populations

Most captures of polar bears were made on land in the Hudson Bay lowlands of north-eastern Manitoba, Canada (Fig. 3-1). This region lies at the boreal forest-tundra ecotone and is characterized by long, cold winters and short cool summers (Thompson 1968). Hudson Bay freezes entirely each winter, with the exception of an offshore lead system (Lardner 1968, Danielson 1971). In summer all the sea ice melts, forcing bears ashore in a relatively restricted area (Stirling et al. 1977). This results in a high density of bears on land during summer and autumn and allows researchers a relatively high catch-per-unit-effort. Logistic centres for field operations were based at the town of

Churchill, Manitoba or in temporary field camps to the south and east of Churchill and within 150 km. Except where noted, all captured bears were located north of the Nelson River at 57° N latitude and south of 59° N latitude. Prior to 1977, most animals handled were captured at or near the town of Churchill as part of a regional bear management program (Stirling et al. 1977). After 1977, and especially after 1980 when my field work began, most bears were handled away from human habitation.

Capture programs were carried out during three seasons, each determined by the seasonal movements and activities of the bears. During February and March (spring season) adult females with their cubs-of-the-year were handled each year soon after they emerged from overwinter maternity dens. The second sampling period occurred in late July and August (summer season) at or soon after the time that the population was forced ashore from the melting sea ice of Hudson Bay. The third sampling period was in October and early November (autumn season) just before Hudson Bay refroze and all bears, except pregnant females, returned to the sea ice.

Spring field work was conducted 8 - 19 March, 1980; 26 February - 25 March, 1981; 13 February - 29 March, 1982; 28 February - 23 March, 1983; and 29 February - 24 March, 1984. Summer field work was conducted on 27 July - 16 August, 1981; 12 July - 8 August, 1982; 29 July - 24 August, 1983; 20 July - 1 September, 1984; and 27 July - 1 September, 1985. Autumn field work was conducted 11 October - 3 November, 1980; 27 September - 4 November, 1981; 28 September - 14 November, 1982; and 12 September - 31 October, 1983.

In the spring field seasons, searches were made for bears or their tracks in snow by flying along water courses and lake shores (Ramsay and Andriashek 1986). The ability to locate bears in spring varied greatly with weather conditions. Field work was discontinued when wind chill values exceeded 2200 watts/m^2 or when visibility while flying was limited. Consequently, many days of aerial search for bears were lost, often consecutively. Bears, or their tracks in snow, were most visible on calm, sunny days immediately following a fresh snowfall. Overcast skies or blowing snow made it considerably more difficult to track and locate bears. All bears observed were captured except those few seen too late in the day to allow complete handling before nightfall. Because spring searches were predominantly conducted on land, usually only adult females and their cubs-of-the-year were available for capture. Consequently, males and females one year of age and older older, except for females with newborn cubs, were rarely sampled then and only during searches made on the sea-ice.

Spring field operations during this study were primarily based at Churchill, although a camp on the Owl River, 100 km southwest of its mouth was also used each year. Consequently, most search effort was concentrated in the more northerly portions of the study region because it was traversed twice daily, on the outbound and return route, resulting in the region south of the Owl River receiving less search effort than in areas further north. At the initiation of this study, however, it was assumed that the distribution of maternity dens would be similar to that described by Stirling et al. (1977) and therefore allocation of considerable search effort into the southern portion of the study area was made each year. Every major water course and lake south of the Owl River was searched two or more times in each spring field season. In addition, in spring of the years 1981 through 1983, personnel of the Government of Manitoba, including some of the same observers that had made the sightings in the previous decade, conducted fixed-wing searches for polar bears in conjunction with our helicopter searches.

During the summer and autumn field seasons all age and sex classes were available for capture. Helicopter searches were made throughout most of the study region. The population tends to segregate by sex in those seasons with most males near the coastline and most females and juveniles distributed inland (Stirling et al. 1977, Lunn and Stirling 1985). In summer, some bears could not be captured because they were found in areas too wet to allow safe immobilization. Most other bears sighted were captured although some bias against sampling adult males occurred because of the importance of obtaining as large a sample of females as possible and the need to spend more time searching for each female located because of the distributional differences between sexes. I have assumed, however, that female bears of each age and reproductive class handled in summer and autumn were sampled at approximately their frequency in the female component of the population and have pooled samples from these two seasons in most of the analyses except for comparisons of body weight.

Calculation of age-specific reproductive rates were made following modifications of the techniques used by Stirling et al. (1980) and Furnell and Schweinsburg (1984). Only data from summer and autumn were used as only during those seasons could the whole population be sampled. Females with yearling cubs were only included in the total number of females of each age class; they were not incorporated in totals of females with cubs because many females abandon their yearling cubs before the summer sampling period (Ramsay and Stirling 1982). Their inclusion in calculation of reproductive parameters would bias estimates downward because it is not possible to differentiate solitary females that had recently abandoned yearling cubs from females that had not had cubs-of-the-year in the previous year. The age-specific rate of litter production (LP) was calculated by the formula:

$$LP_x = \frac{\text{No. of females of age x with cubs-of-the-year}}{\text{No. of females of age x}}$$

The age-specific mean litter size (LS) was calculated by the formula:

$$LS_x = \frac{\text{No. of cubs-of-the-year accompanying females of age x}}{\text{Total no. of cub-of-the-year litters with females of age x}}$$

An estimate of age-specific natality rate is the product of these two reproductive parameters. Stirling et al. (1980) calculated LP for females in the year they conceived whereas I have calculated it for the year they gave birth. The results are comparable although those presented in Stirling et al. (1980) are shifted back one age-class relative to those presented here. Furnell and Schweinsburg (1984) also only considered females with cubs-of-the-year when calculating LP, however, they do not break their sample up by age-class.

Data collected from live-handled polar bears from more northerly populations in the Canadian Arctic are presented for purposes of comparison or to augment data that could not be collected within the study population because of logistic constraints. These supplementary data were collected as part of other research programs conducted by the Canadian Wildlife Service and the Northwest Territories Wildlife Service and some have not been published previously. Descriptions of these study regions and methods of capture of the bears there are described in DeMaster et al. (1980), Stirling et al. (1980, 1984), Schweinsburg et al. (1982), Furnell and Schweinsburg (1984), and Amstrup et al. (1986).

3.2.2 Capture and handling

Bears were captured alive using standard chemical immobilization methods (Lentfer 1968, Larsen 1971). Most animals were located during search operations carried out in a Bell 206B helicopter and subsequently shot from the air with darts containing immobilizing drugs. Bears located in the vicinity of the town of Churchill were captured in baited snares or culvert traps and subsequently drugged, or were shot with immobilizing darts fired from a motor vehicle. Immobilizing drugs used and specific handling details varied somewhat over the 20 years (1966 - 1985) that data were collected (Ramsay and Stirling 1986b).

Once safely immobilized, each bear was assigned a permanent and unique identifying number on its first capture by which it could be identified on any subsequent recapture. The identifying number was applied as a tattoo on each upper lip and with a plastic or metal tag attached in each ear (Stirling et al. 1977). Each bear's sex and the age and sex of accompanying bears were recorded. Morphometric measurements were taken and a first premolar tooth extracted for age determination through counts of cementum annuli (Stirling et al. 1977, Grue and Jensen 1979). A temporary number was painted on the pelage of the back and/or sides using a hair dye. This facilitated identification of individuals from afar during the season of capture. Selected adult females were fitted with radio transmitter collars in the 164 MHz range to facilitate relocation or recapture of the animals when desired. Weights of cubs-of-the-year less than six months old were determined to the nearest 100 gm using a spring scale. A spring scale was also used to determine body weights, to the nearest kilogram, of a representative sample of bears; these data were then used to generate a best-fit regression of body weight on axillary girth (Nagy et al. 1984). All body weights of bears reported in this paper, except those younger than six months of age, were estimated using the regression formula. Axillary girth was measured when the bears were in a sternally recumbent position with limbs extended away from the body and along the longitudinal axis. A cord was passed under the body in the axillary region and the smallest body circumference recorded during an exhalation of the bear. A tension of approximately 600 gm was maintained on the cord during measurement.

Not all measurements could be obtained for every bear and some radio-tagged animals were sighted on occasion but not handled. Consequently, for each age and sex class of bear, not all sample sizes were the same for each parameter measured.

Two cubs found dead in spring were kept frozen and air freighted to Edmonton, Alberta. There they were necropsied by Dr. D. Onderka of Alberta Agriculture. Standard anatomical and histological necropsy procedures were used.

Blood samples were obtained from free-ranging female bears older than six months of age by femoral venipuncture using a 50 ml syringe. Whole blood was immediately transferred to sterile vacutainers and stored at approximately 0° C until the evening of the day collected. Samples were then centrifuged and the serum removed and frozen at -20° C until analysis. Serum levels of progesterone were determined at the Reproductive Endocrine Laboratory of the University of Saskatchewan using antisera prepared in rabbits (Foresman and Daniel 1983, Rawlings et al. 1984). All samples were run in duplicate against known standards. Bears were divided into seasonal, age, and reproductive classes for comparison of progesterone levels. Those four years of age and older were considered adults; those younger than four years were considered juveniles. Adult bears were further subdivided by whether they were accompanied by cubs of any age. Juvenile bears were never accompanied by their own cubs. The seasonal strata were the same as those used for other analyses.

All statistical calculations were made using MIDAS (Statistical Research Laboratory, The University of Michigan) or BMDP (Department of Biomathematics, The University of California, Los Angeles) statistical software.

3.3 Results

3.3.1 Population description

Eight hundred and ninety-five individual females including 230 cubs-of-the-year and 90 yearling cubs were captured in the population studied between 1966 and 1985 (Table 3-1). Seventy percent of these females (626/895) were handled between 1980 and 1985, the major years of this study. Eight hundred and thirty-five males have also been captured since 1966, including 205 cubs-of-the-year and 90 yearling cubs. Because bears were handled in three discrete annual field seasons, an individual could be captured or observed more than once in a single year. Before 1980, and especially prior to 1977, most bears were handled in autumn at or near Churchill, Manitoba as part of a bear monitoring program (Stirling et al. 1977). Bears near Churchill were, on average, significantly younger than bears in the study population captured away from human habitation (Stirling et al. 1977, Lunn and Stirling 1985). Hence, the apparent absence of older bears in the annual samples prior to 1977 is probably due to biases introduced by the sampling method and probably does not represent missing age classes from the population in those years.

The terrestrial boundaries of the study population are known only approximately. The northern limit occurs along the western coast of Hudson Bay in the Northwest Territories. Few captures of bears were made north of Churchill and none in that portion of the Northwest Territories. Ground and aerial searches for tracks of families in spring produced no evidence to suggest that any females in this population had maternity dens north of Churchill (Northwest Territories Wildlife Service, unpublished reports). Between 1976 and 1983, a total of 517 bears were reported killed by Inuit hunters from the four communities along the west coast of Hudson Bay, north of Churchill (Fig. 3-1). The proportion of previously marked animals in the sample from each of the three more southerly communities declined slightly from south to north (Table 3-2). At Chesterfield Inlet, the community furthest removed from the centre of marking activity in Manitoba, the proportion of tagged animals was markedly lower than was the sample in the other three communities, suggesting that for most bears the northern boundary of the population lay somewhere near Chesterfield Inlet. Communities further north reported killing either no bears or far fewer than 1% of their annual quota that were marked in Manitoba.

The southern boundary of the population is also poorly defined although it appears to lie northwest of the Ontario - Manitoba border (Fig. 3-1). In 1984, the Ontario Ministry of Natural Resources began capturing and marking polar bears along that province's Hudson Bay coast. Of 151 bears captured and marked in Ontario in 1984 only seven (4.6%) were originally marked in Manitoba. Similarly, of 131 bears handled in Manitoba in 1985, only one (0.8%) was initially marked in Ontario. To put these figures in perspective, the recapture rate of polar bears in Manitoba during the same period was 86 recaptured of 231 handled (38%) in 1984 and 63 recaptured of 131 handled (48%) in 1985.

Although the boundaries of the polar bear population when on shore along western Hudson Bay require further definition, their location should improve with data from future studies. Little is currently known of the distribution of bears in this or neighbouring populations when on the ice of Hudson Bay.

3.3.2 Weight estimation

Scale weights and axillary girths were available for 138 bears ranging in age from cubs-of-the-year to 18 years. Weights of bears in this sample ranged from 36 to 409 kg and axillary girths ranged from 48 to 165 cm. For both sexes pooled, the best fitting polynomial regression model was

$$\ln SWT = 0.02 + (0.062 \cdot AXG) - (0.000165 \cdot AXG^2); \qquad r^2 = 0.98$$

where ln SWT = the logarithm of scale weight in kg and AXG = axillary girth in cm. All weights presented, other than those for cubs-of-the-year in spring, were calculated using this model.

3.3.3 Age-specific reproductive parameters

One hundred and eighteen adult females with accompanying cubs-of-the-year and eight solitary adult females were handled in spring in the inland denning region of northwestern Manitoba between 1980 and 1984 (Table 3-3). The mean age of females with cubs-of-the-year was 13.6 years (S.E. = 0.44, median age = 14.0 years), significantly younger than that of solitary adult females ($\bar{X}$ age = 18.0 years, S.E. = 2.4; Mann-Whitney U = 276, $P = 0.05$). Inter-year differences in the mean age of bears with cubs varied little (Kruskal-Wallis H = 6.61, df = 4, $P = 0.16$), ranging between 15.4 (S.E. = 1.1) years in 1982 to 12.0 (S.E. = 1.1) years in 1984. There were significant differences, however, in the mean ages of females with differing sized litters (Kruskal-Wallis H = 6.07, df = 2, $P = 0.05$). Females with litters of three or four cubs ($\bar{X}$ age = 16.3 years, S.E. = 0.9) were older, on average, than females with twin cubs ($\bar{X}$ age = 13.0 years, S.E. = 0.5, $t_{115} = 2.4$, Bonferroni $P = 0.05$). There was no significant difference between the mean ages of females with litters of one ($\bar{X}$ age = 14.3 years, S.E. = 1.2) and two ($t_{115} = 1.2$, Bonferroni $P = 0.7$) or three or four ($t_{115} = 1.2$, Bonferroni $P = 0.7$) cubs. More than two-thirds of females with litters of three or four cubs were older than the median age. The increased incidence of these largest sized litters in older age classes accounts for the general increase in mean litter size with age.

During summer and autumn, a total of 129 adult females were captured while accompanied by cubs-of-the-year and a further 46 while accompanied by yearling cubs (Table 3-4). No adult females were ever seen accompanied by cubs older than yearlings during these seasons. The average age of females with cubs-of-the-year ($\bar{X}$ age = 11.4 years, S.E. = 0.4, median age = 11.0 years) did not differ from the age of females with yearling cubs ($\bar{X}$ age = 11.6 years, S.E. = 0.6, median age = 11.0 years) (Mann-Whitney U = 2867, $P = 0.85$). In addition, the average age of females with cubs-of-the-year did not differ from that of females with yearlings in the years that their cubs were born (Mann-Whitney U = 1762, $P = 0.25$). The ages of females with different sized litters did differ significantly, however, for those with cubs-of-the-year (Kruskal-Wallis H = 13.5, df = 2, $P = 0.001$) but not for those with yearling cubs (Kruskal Wallis H = 1.1, df = 2, $P = 0.58$). The mean age of females with single cubs-of-the-year ($\bar{X}$ age = 10.1 years, S.E. = 0.5) was less than that of females with two cubs ($\bar{X}$ age = 12.4 years, S.E. = 0.6 $t_{124} = 3.1$, Bonferroni $P < 0.01$) and three cubs ($\bar{X}$ age = 14.0 years, S.E. = 0.9, $t_{124} = 2.6$, Bonferroni $P < 0.05$).

The average age of females with cubs-of-the-year in summer and autumn was markedly younger than that observed in spring (Mann-Whitney U = 9768, $P < 0.001$). Twelve percent (14/118) of the bears with cubs-of-the-year in spring were 20 years or older and 28% (33/118) were 10 years or younger. By summer/autumn, these proportions were 4% (5/129) for bears 20 years or older and 47% (61/129) for those 10 years or younger.

The age structure of female subadult and adult bears handled in northeastern Manitoba in summer and autumn (Table 3-4) allowed calculation of age specific reproductive parameters for the population (Table 3-5). Onset of cub production was age-specific and sudden. No three year-olds and only 5% of four year olds were with cubs in summer and autumn, whereas almost 50% of bears aged five years and older had accompanying cubs. Onset of reproductive senescence appeared similarly sudden. No bears older than 20 years in summer and autumn had accompanying cubs even though bears older than 20 years were known to have cubs with them in spring (Table 3-3). Females older than about 20 years apparently experienced higher levels of cub loss before summer than did younger bears, although sample sizes were small.

As both the rate of litter production and mean litter size tended to increase with age, from first parturition to reproductive senescence, overall natality rates also increased with age. The inverse of rate of litter production is the interbirth interval or time between successive litters. The clustering of litter production rates around 0.5 for all productive age-classes suggests that a two-year breeding interval is common.

3.3.4 Interbirth interval and age of weaning

Sixty-six times in the western Hudson Bay population, adult females were captured on two separate occasions, each time with cubs of different litters (Table 3-6). The mean maximum interval between successive litters, calculated from these longitudinal observations was 2.9 years. Because some intervening litters were likely undetected, especially during the longer intervals, the actual mean interbirth interval was probably lower. The most striking aspect of these data is that almost 40% of the cycles observed were two years in length. In contrast, of 26 interbirth intervals recorded from more northerly Canadian populations, only five (19%) were two years in length. A female with a two-year interbirth interval would have to mate in the spring of the year when her cubs were about 16 months old (yearlings). Adult females apparently abandon cubs from previous litters before entering their maternity dens, as none in dens has ever been recorded accompanied by cubs of different ages. Cubs would therefore have to be abandoned as yearlings for females to have two-year interbirth intervals.

Consistent with a high proportion of females having two-year interbirth intervals, 55% of all yearling cubs captured in this population during summer or autumn were independent of their mothers (Table 3-7) In more northerly populations independent yearlings are rare; only seven out of 210 (3%) were independent in spring. Even the proportion of two-year old cubs that were independent in spring in those populations, 42% (92/225), was lower than that of yearling cubs during summer/autumn in western Hudson Bay. Independent yearling cubs from western Hudson Bay in summer and autumn appeared to have at least as great a probability of survival to 2 years-of-age or older (39/93 = 0.42), a minimum estimate of survival rate, as did yearling cubs still with their mother (25/76 = 0.33) ($G = 1.5$, df = 1, $P = 0.23$). There was no significant difference between sexes in the proportion of yearlings that were independent when captured ($G = 0.27$, df = 1, $P = 0.60$).

3.3.5 Body weight of adult females

Adult females lost weight through summer and autumn, when they were on land and without access to seals (Table 3-8). Solitary females showed the least change (-8%, $F_{1\ 56} = 1.92$, $P = 0.17$); females with cubs-of-the-year the greatest (-20%, $F_{1\ 11} = 40.7$, $P < 0.001$). Females with yearling cubs showed an intermediate weight loss between those seasons (-11%, $F_{1,31} = 6.1$, $P = 0.02$). Solitary females were significantly heavier than females with cubs in both summer ($F_{2,81} = 20.5$, $P < 0.001$) and autumn ($F_{2,87} = 49.9$, $P < 0.001$); females with cubs-of-the-year and yearling cubs were not significantly different in weight, even in autumn ($t_{87} = 1.84$, Bonferroni $P > 0.05$).

The sample of solitary females handled in summer and autumn probably included both pregnant and non-pregnant females. Sixteen adults that were known to be pregnant were captured in the autumn period. Their mean weight was 234 kg (S.E. = 8.2), about 75 kg (45%) greater than the mean weight of females with cubs of the year in spring. This difference presumably represents the average cost of maintenance as well as producing and nursing cubs over winter until feeding is resumed.

Adult females from western Hudson Bay in spring, with cubs-of-the-year, weighed an average of 159 kg (Table 3-8), ranging from 94 to 233 kg. Older females tended to be heavier than younger females

$$WT = (2.2 \cdot AGE) + 128; \quad r^2 = 0.20,$$

where WT represents body weight in kg and AGE is in years. An even stronger weight:age relationship was detected among solitary adult females in autumn, the reproductive class that includes all pregnant females. Once again, older bears tended to be heavier than younger adults

$$WT = (6.5 \cdot AGE) + 171; \quad r^2 = 0.43.$$

Three solitary females that were $\geq$ 20 years of age had a mean weight in autumn of 157 kg (S.E. = 12), about one-half that expected from the weight - age regression for younger adults, and were not used in the regression. It would appear that the sudden onset of reproductive senescence among bears older than 19 years is correlated with a notable drop in body weight. No similar weight:age relationship was apparent for females with cubs-of-the-year or yearling cubs in either summer or autumn (all $r^2 < 0.02$).

Because most sampling in western Hudson Bay was done in the late summer and autumn while in other regions of the Arctic it was done in the spring, comparisons of body weight of animals of different age and sex classes among populations are difficult. The limited comparative data available, however, indicate little difference in seasonal weights between the two regions. Four known-pregnant bears from western Hudson Bay that were handled in summer had a mean weight of 274 kg (S.E. = 27); six known-pregnant females handled in summer from more northerly populations had a mean weight of 257 kg (S.E. = 8), a difference that was not significant ($t_8 = 0.7$, $P = 0.5$). Females with cubs-of-the-year in the northern populations had a mean weight of 218 kg (S.E. = 12, $n = 18$) in summer and 208 kg (S.E. = 14, $n = 4$) in autumn; females with yearling or two-year old cubs had a mean weight of 210 kg (S.E. = 8, $n = 17$) in summer and 195 kg (S.E. = 15, $n = 7$) in autumn. Only for females in spring with cubs-of-the-year were there sample sizes large enough to allow reasonable comparison. Those in the northern populations had a mean weight of 161 kg (S.E. = 2; $n = 191$), no different in weight from their counterparts in western Hudson Bay ($t_{307} = 0.5$, $P = 0.62$).

The greatest increase in weight occured between the spring and summer sampling periods, with the largest gains achieved by pregnant females. Unfortunately, there were few spring weights for breeding females from the western Hudson Bay population. Twenty-four females from the northern populations were known to have bred in the year of their sampling, at or about the time of their oestrus. They had a mean weight of 166 kg (S.E. = 26), little different from the weight of females with cubs-of-the-year in those populations, but significantly lower than that of known-pregnant females in summer/autumn ($t_{28} = 8.0$, $P < 0.001$). Although the sample is not from western

Hudson Bay, it would appear that the annual period of peak weight gain for pregnant females occurs after they have mated. Weight gains experienced by pregnant bears during the period of hyperphagia can be large. Solitary, and presumed pregnant, females in summer were often obese to the point of inhibiting locomotion (Plate 3-1). One 17 year old female from western Hudson Bay with three cubs-of-the-year was handled in November, 1983 when she weighed 99 kg. The following July she was without cubs, probably pregnant, and weighed 410 kg, a four-fold weight change in eight months.

In both summer and autumn, mean weights in 1983 for all reproductive classes of adults in western Hudson Bay were lower, but in most cases not significantly so, than in other years sampled. Known-pregnant females handled in autumn, 1983 were significantly lighter in weight ($\bar{X}$ weight = 216 kg, S.E. = 9.8, n = 8) than were known-pregnant bears handled in autumn of other years ($\bar{X}$ = 253 kg, S.E. = 9.5, n = 8; t_{14} = 2.7, P = 0.01). Bears of all age and sex classes in the summer and autumn of 1983 appeared to us, at the time of capture, to be, on average, in poorer condition than at equivalent seasons in the years previous and subsequent. Some qualitative behavioural observations corroborated this view. During autumn, 1983 the town of Churchill recorded a larger number of bears feeding at its dump (Lunn and Stirling 1985) than in the previous three years and a higher number of human - bear incidents than in any year of the previous decade. Three cubs-of-the-year were found abandoned by their mothers in autumn and near starvation, something seen in no other year.

There were significant differences in mean weights in spring among years ($F_{4\ 113}$ = 2.4, P = 0.05) but not among bears with differing sized litters ($F_{2\ 115}$ = 1.6, P = 0.20). Females with cubs-of-the-year in spring, 1984 were lower in weight ($\bar{X}$ weight = 145 kg, S.E. = 5.9) than in any other year sampled. The differences among years were only significant, however, between bears handled in 1984 and 1982 ($\bar{X}$ weight = 171 kg, S.E. = 4.3, t = 3.0, Bonferroni $P < 0.05$).

3.3.6 Litter size and cub survival

Litters of two were predominant in western Hudson Bay in spring (Fig. 3-2) and one litter of four was observed. The mean size of litters in spring was 1.93 (S.E. = 0.05) with little inter-year variation and no significant difference in size among years ($F_{4, 113}$ = 0.23, P = 0.92). Sizes of litters in spring generally increased with the age of the mother until age 20 years and then declined (Table 3-3). The proportion of females that had litters of two cubs remained relatively constant at about 0.7 for all age classes between five years and 19 years (5 to 9 years - 0.71; 10 to 14 years - 0.75; 15 to 19 years - 0.70; ≥20 years - 0.36), whereas the increase in frequency of litters of three or four cubs in the mid-range of age-classes was coupled with a decline in frequency of females with litters of one cub in the same age-classes.

By summer/autumn (Fig. 3-2) the mean size of cub-of-the-year litters had declined to 1.60 (S.E. = 0.05), a 17% decline and significantly different from that in spring ($F_{1, 245}$ = 18.9, $P < 0.001$). The mean size of yearling-cub litters in summer/autumn was 1.68 (S.E. = 0.05), not significantly different from that of cubs-of-the-year then (Table 3-4). Between spring and summer/autumn the proportion of triplet and twin cub-of-the-year litters decreased and that of singles increased. Females that had lost their entire litter during that period were not considered when calculating summer/autumn mean litter size, consequently, early cub loss would have been even greater than that indicated by differences in mean seasonal litter size. An approximate estimate of entire loss of cub-of-the-year litters was determined from 19 females captured, and two females with radio collars sighted, in spring that were recaptured or resighted the subsequent summer or autumn. Four (19%) lost their entire litter before the cubs were one year old.

The marked drop in mean cub-of-the-year litter size between spring and summer/autumn indicates that considerable cub mortality occurred in the first few months after emergence from dens. The number of cubs initially marked that were subsequently relocated in a later season gives a minimum estimate of cub survival. Absence of a resighting is not confirmation of death, but a resighting is confirmation of survival. Presumably, the longer the interval since initial capture, the greater the opportunity for survivors being resighted. Forty-one (18%) of cubs-of-the-year initially captured in spring were recorded alive the following summer or later, at least five months after capture. There was no difference in the proportion of cubs that survived by sex (G = 0.39, df = 1, *P* = 0.75) or litter size in spring (G = 3.0, df = 2, *P* = 0.22). Cubs-of-the-year handled in summer/autumn were 2.5 times as likely to be resighted one year or more later than those initially handled in spring (Table 9), a difference that is highly significant (G = 14.0, df = 1, $P < 0.001$) and further indication of extensive cub mortality before summer of their first year. No differences in minimal survival rates were found between male and female cubs-of-the-year for either season of capture (in spring G = 1.3, df = 1, *P* = 0.25; in summer/autumn G = 0.23, df = 1, *P* = 0.63). For these analyses, however, cubs handled in spring had a longer interval until the first opportunity for resighting than did cubs handled in summer/autumn.

The estimated survival rate of cubs continued to increase with age. For yearling cubs handled in summer or autumn (1966 - 1984) the minimum survival rate, to at least the next year, was 0.38 (64/169); that for two-year-old cubs was 0.53 (71/134). Data that are directly comparable to these are unavailable from more northerly polar bear populations as so few animals were captured there in summer and autumn. For bears handled in spring in those populations, however, the minimum rate of survival to at least the next year was 0.16 (53/340) for cubs-of-the-year, 0.21 (38/182) for yearling cubs, and 0.28 (56/197) for two-year-old cubs, suggesting that cub survival rates may be higher in western Hudson Bay than in other Canadian populations for all age-classes of cubs.

A direct measure of early cub mortality in western Hudson Bay was obtained from the nineteen adult females that were handled in spring with cubs-of-the-year and subsequently recaptured in summer/autumn of their year of capture. Eleven of these females lost cubs including three that lost their entire litter, for a net cub mortality of 38% (14/37) (Fig. 3-3). Females that lost no cubs were significantly heavier in spring ($\bar{X}$ weight = 185 kg, S.E. = 11.7) than were females that lost at least one cub ($\bar{X}$ weight = 150 kg, S.E. = 3.8, Mann-Whitney U = 76.5, P = 0.007). Females that lost two cubs were similar in weight to those that lost one. The age of the mother appeared a less important factor than did weight in predicting cub mortality as there was little difference in age between females that lost no cubs ($\bar{X}$ age = 13.4 years, S.E. = 1.4) and those that did ($\bar{X}$ age = 11.4, S.E. = 1.5, Mann-Whitney U = 55.5, P = 0.34).

Few cubs that died of natural causes were found in western Hudson Bay. Two adult females, aged seven and 11 years, were captured at their dens in spring, each with a single dead cub-of-the-year. These were the two youngest solitary females listed in Table 3-3. Laboratory necropsies on their cubs did not reveal cause of death in either case. The carcass with the younger mother was much lighter in weight (3.2 kg) than was the mean weight of living cubs from litters of one (14.2 kg), and, in fact, lighter than any cub captured alive. Time of death relative to parturition was not known, however, and the cub may have died before the sampling period when cub weights would have been lower. The heavier of the dead cubs was of similar weight (12.2 kg) to cubs captured alive. Both carcasses had internal and subcutaneous fat reserves, especially evident in the larger cub. The smaller cub's digestive tract was devoid of ingesta while the larger had milk residues in the intestines. All tissues were found to be negative for *Trichinella* spp. larvae, no significant bacteriological infections were detected, no sign of other internal parasites were found, and no visible lesions were seen. The lighter cub's death may have been a result of the mother being analactic; her mammae were undeveloped and no milk could be expressed. If her cub's death was well before our discovery, however, mammary regression would probably have occurred. Analactia seems a less likely explanation for the death of the heavier cub as its mother's anterior pair of mammae were enlarged and milk could be easily expressed.

Wolves (*Canis lupus*) were documented in spring harassing polar bears, and in one case killed a cub of a family travelling to Hudson Bay (Ramsay and Stirling 1984). One dead cub was found in October, 1982 near Churchill. Necropsy revealed thoracic puncture wounds and haemorrhaging from the liver. The wounds were of a size and conformation that they could have been inflicted by a wolf or a subadult bear.

Some cubs may be abandoned or become prematurely separated from their mother. A single cub-of-the-year was found walking alone in March 1981. No adult female was found in the vicinity although tracks of an adult with one cub passed nearby. Ambient temperatures at the time of location were about -30° C and, to still be alive, the cub must have nursed within a relatively short time prior to discovery (Blix and Lentfer 1979).

The total number of cubs born each year in the western Hudson Bay population is not known. Assuming no immigration, a minimum estimate of a cohort's size would be the total number of bears, handled at least once, from that cohort during the expected lifespan of its members. The number captured must be an underestimate because of cumulative mortality and because some bears would remain uncaptured. Of the cohorts born between 1980 and 1984 inclusive, 72 bears have been captured to 1985 from the 1980 cohort, 90 from those born in 1981, 93 from those born in 1982, 115 from those born in 1983, and 63 from those born in 1984. Thus, 54% of all bears captured from the 1980, 1981, 1983, and 1984 cohorts were first captured as cubs-of-the-year in spring of their birth year, while the comparable figure for 1982 was 33%.

3.3.7 Weight and sex of cubs

Weights of living cubs-of-the-year in spring from western Hudson Bay ranged between 3.4 kg for a triplet cub in 1981 and 24.5 kg for a single cub in 1980 with an overall mean weight over five years of 10.9 kg (Table 3-10). Mean cub weights differed significantly among years ($F_{4,\ 210} = 5.35$, $P < 0.001$). Cub weights in 1984 were significantly lower than in 1981 ($t_{210} = 4.5$, Bonferroni $P < 0.001$) and 1983 ($t_{210} = 3.3$, Bonferroni $P < 0.05$) and marginally lower than in 1982 ($t_{210} = 2.6$, Bonferroni $P < 0.1$).

Single cubs in spring were about 30% heavier than were individual cubs from a litter of two and a twin cub about 30% heavier than was a cub from a litter of three (Table 3-10). Thus, the ratio of mean weight of cubs from adjacent sized litters was close to 1.3, a pattern consistent for all years save 1982 when the ratio for mean single cub weight to twin weight was 1.0 and that of mean twin weight to triplet weight was 1.8. As expected with a volumetric relationship of 1.3, the straight-line length of cubs varied significantly among litters of differing sizes by a ratio of 1.1 ($F_{2,\ 219} = 34.3$, $P < 0.001$; single cubs $\bar{X}$ length = 79.8 cm, S.E. = 1.7; twin cubs $\bar{X}$ length = 74.5 cm, S.E. = 0.4; and triplet cubs $\bar{X}$ length = 66.4 cm, S.E. = 1.5). The total weight of cubs from a litter of two was almost 60% greater than that of a single cub and the total weight of cubs from a litter of three was about 80% greater. The total weight of a litter of three was about 10% greater than that of a litter of two.

Cubs from western Hudson Bay that were initially handled in spring and known to have survived to at least one year were significantly heavier ($\bar{X}$ weight = 12.4 kg, S.E. = 0.5) than those that were not resighted at age one year or older ($\bar{X}$ weight = 10.6 kg, S.E. = 0.2, $F_{1,\ 213} = 10.5$, $P = 0.001$). Cubs in spring, 1984, were, on average, lighter in weight than were cubs in other years and had the least opportunity to be resighted, hence they could bias the weight downward of bears never resighted. When only cubs tagged in the springs of 1980 through 1983 were considered, there was still a significant difference in weight between the two classes ($F_{1\ 179} = 6.7$, $P = 0.01$).

Even in spring, sexual dimorphism in weight was apparent and female cubs were about 8% lighter than were male cubs ($t_{213} = 1.9$, $P = 0.06$) (Table 3-10). Although the sex ratio of the samples of cubs varied among years, from 0.82 to 1.33, it was unity (114 males:114 females) for the combined five years of sampling. The lowest sex ratio occurred in 1984, the year that cub weights were also lowest; however the sex ratio was also low in 1981 (0.89), the year with the highest mean weight of cubs. No difference in spring sex ratio was discernable among litters of differing sizes ($G = 3.0$, $df = 2$, $P = 0.22$). The sex ratio for cubs-of-the-year captured in summer and autumn was 0.72, and that for yearlings 0.96.

If polar bear twins are primarily dizygotic then the expected frequency of sex composition of litters of two should be 1:2:1 for all female, mixed sex, and all male litters respectively. In contrast, if twins are primarily monozygotic then a 1:1 frequency of all female and all male litters of two would be expected. The observed sex composition of litters of two in spring was 21 all female, 30 mixed sex, and 27 all male, not significantly different from the expected pattern for dizygotic twins ($\chi^2 = 5.1$, $df = 2$, $0.1 > P > 0.05$). Litters of three did not vary significantly from the 1:3:3:1 frequency of sex composition expected if the litters were trizygotic; four all female litters, five with two females and one male, four with one female and two males, and one all male ($\chi^2 = 3.5$, $df = 3$, $P > 0.1$).

Between spring and summer, cubs-of-the-year showed a five-fold increase in weight and then, like adult females, showed a significant decline in weight between summer and autumn during the on-land period (Table 3-11). Yearling cubs showed a similar weight loss during the on-land period. The mean summer to autumn weight loss was about 20% for cubs-of-the-year ($F_{1\ 125} = 21.4$, $P < 0.001$) and 18% for yearlings ($F_{1\ 90} = 11.1$, $P = 0.001$). Females were lighter in weight than were males for both age classes and seasons of sampling, although such sexual dimorphism was less pronounced in summer (for cubs-of-the-year $F_{1,66} = 2.3$, $P = 0.14$; for yearlings $F_{1,26} = 1.6$, $P = 0.22$) than in autumn (for cubs-of-the-year $F_{1,57} = 3.5$, $P = 0.07$, for yearlings $F_{1,62} = 14.3$, $P < 0.001$). No significant differences were detected in the summer/autumn mean weights of cubs of either age among years or seasons.

Yearlings that were known to survive to at least 2 years of age tended to be heavier ($\bar{X}$ weight = 119.0 kg, S.E. = 5.2, $n = 32$) than were bears that were not seen again ($\bar{X}$ weight = 107.1 kg, S.E. = 3.6, $n = 82$; $t_{112} = 1.8$, $P = 0.08$). Solitary yearling females were not significantly lighter in weight ($\bar{X}$ weight = 88.0 kg, S.E. = 6.3, $n = 29$) than were yearling females still with their mothers ($\bar{X}$ weight = 105.2 kg, S.E. = 5.0, $n = 27$; $t_{110} = 2.2$, Bonferroni $P > 0.05$). Similarly, solitary yearling males were little different in weight ($\bar{X}$ weight = 123.5 kg, S.E. = 4.7, $n = 34$) from those still with their mother ($\bar{X}$ weight = 125.0 kg, S.E. = 5.5, $n = 24$; $t_{110} = 0.2$, Bonferroni $P > 0.5$).

Although a much higher proportion of yearling cubs were independent of their mothers in western Hudson Bay relative to more northerly populations, weights of cubs differed little between the two regions. Yearling females from the northern populations had a mean weight of 114 kg (S.E. = 7, $n = 14$) in summer and male yearling cubs had a mean weight of 130 kg (S.E. = 10, $n = 10$), neither value significantly different from their counterparts in western Hudson Bay (for females $t_{21} = 0.5$, $P = 0.61$; for males $t_{22} = 0.3$, $P = 0.80$).

A crude index of the extent of female investment in cubs is the ratio between weight of litters and weight of mothers in spring. This is not an ideal measure of reproductive investment as it does not consider allometric metabolic costs that would be associated with cubs of differing sizes nor possible differences in foetal growth rates with increasing litter size. I chose to use this simple statistic, however, because 1) litter sizes varied little among years, even in years with significant differences in cub weights; 2) it is an easily obtained measure that permits comparison to be made among populations;

and 3) more detailed information on energetics of polar bears is needed before a better measure of reproductive investment can be applied. In western Hudson Bay, the ratio of litter weight to mother weight was 0.13 (S.E. = 0.004) with little inter-year variation ($F_{4,106} = 1.07$, $P = 0.37$). Ratios among females with differing litter sizes, however, varied greatly ($F_{2,101} = 54.2$, $P < 0.001$). Females with one-cub litters had the lowest mean ratio ($\bar{X} = 0.08$, S.E. = 0.004), significantly lower than that for females with twins ($\bar{X} = 0.14$, S.E. = 0.003, $t = 8.5$, df = 108, Bonferroni $P < 0.001$) or triplets ($\bar{X} = 0.16$, S.E. = 0.007, $t = 8.5$, df = 108, Bonferroni $P < 0.001$). Females with twins and triplets were more similar ($t = 2.3$, df = 108, Bonferroni $P < 0.1$).

3.3.8 Serum progesterone concentration

Clear differences in the seasonal pattern of serum progesterone (Fig. 3-4) were observed for solitary females four years of age and older ($F_{2,74} = 37.0$, $P < 0.001$), with an increase in levels from spring ($\bar{X} = 1.1$ ng/ml, $n = 63$) through summer ($\bar{X} = 5.3$ ng/ml, $n = 19$) and autumn ($\bar{X} = 15.7$ ng/ml, $n = 28$). Little seasonal change was apparent, however, for juveniles (spring $\bar{X} = 0.3$ ng/ml, $n = 17$; summer $\bar{X} = 0.4$ ng/ml, $n = 20$; autumn $\bar{X} = 0.4$ ng/ml, $n = 34$; $F_{2,68} = 0.9$, $P = 0.41$) or females with cubs (spring $\bar{X} = 0.5$ ng/ml, $n = 90$; summer $\bar{X} = 0.4$ ng/ml, $n = 30$; autumn $\bar{X} = 0.7$ ng/ml, $n = 34$; $F_{2,128} = 2.2$, $P = 0.12$). Six anomalously low values were recorded for solitary bears in summer and autumn. Two of these bears were from the youngest adult age class (four years) and two were from amongst the oldest (21 years). The remaining two were 12 and 16 years of age. A single 10 year-old female with one yearling cub showed an anomalously high progesterone level in autumn as did a single three year-old juvenile. The anomalous female with yearling cub was characterized, at handling, by a swollen and inflamed vulva with copious mucoid vaginal discharge. No other female handled was observed with similar symptoms.

Fifteen adult females in summer and autumn were known to have been pregnant at the time of sampling and all had serum progesterone levels greater than 2 ng/ml. All were solitary when captured and their progesterone levels were similar to those of most other solitary adult females captured at the same season but whose reproductive status was not known. Eighteen adult females that were without cubs and sampled in spring (18/63 = 0.29) were with an adult male consort when captured (Fig. 3-4). Only one of these females had serum progesterone levels greater than 2 ng/ml although six others had levels ranging between 3 and 5 ng/ml, as high as those of known-pregnant bears in summer (Fig. 3-4).

A more fine scale resolution of temporal changes in serum progesterone levels of solitary adult females within and between seasons is shown in Fig. 3-5. If the six anomalously low progesterone values of summer and autumn are not considered, then the coefficient of the best-fitting linear regression is 0.8. The spring samples with progesterone values greater than 2 ng/ml tend to be clustered higher than the other spring samples. Samples with these moderately elevated values occur throughout the same period when consorting pairs were observed.

One four year-old solitary female was captured in September near Churchill, as part of that town's bear deterrent program, and held in captivity for 51 days until release. Blood samples were obtained on days 42, 46, 49, and 51 of captivity. Serum progesterone levels declined continuously over the sampling period, from 15.0 to 6.4 ng/ml suggesting that, if pregnant, she may have aborted during captivity and repeated handling. An adult female with two cubs-of-the-year, also temporarily held in captivity, was sampled on the same dates and showed consistently low serum progesterone levels ranging between 0.1 and 0.2 ng/ml.

3.3.9 Activities of adult females in spring

After emergence in spring, families spent several days at their den and its immediate vicinity before moving off to Hudson Bay. Post-emergence tenure at dens was apparent from the extent and density of tracks and diggings in the immediate vicinity. Although individual families at dens were not routinely monitored, nine were sighted at den sites several days before capture or den abandonment. Three families spent at least five, six, and seven days respectively, three more families at least eight days, two families at least ten days, and one family at least 12 days at their dens after emergence. These are minimum estimates as all but two of the families were captured while still at their dens and those two may have left prematurely because of our activities. Also, the date of emergence was known exactly for only two of the families.

As might be expected, date of capture and activity of families were related. The median date of capture of families at dens (10 March) was earlier than that of bears travelling when captured (15 March, Mann-Whitney U = 1120, $P = 0.06$). The earliest field searches were conducted on 18 and 19 February, 1982 when only one family was tracked and one recently opened den seen. By 26 February, 1982 and subsequently, both tracks and bears at dens were regularly seen during flights over the denning area. In other years the first field searches were conducted on 8 March, 1980, and 26, 28, and 29 February in 1981, 1983, and 1984, respectively. In each of those years several family groups were observed at den sites and several others were detected already walking toward the coast on the first day of searching. It is not known when the earliest or latest emergence occurred each year as new bears and their tracks were detected as soon as field operations began each year and continued through to the end of the field operations, the peak frequency of sightings was always in early March. Therefore, some unknown number of bears were probably unavailable for capture because they emerged and moved to the sea ice either before or after the period of field operations.

Females that were captured at dens with cubs were heavier ($\bar{X}$ weight = 167 kg, S.E. = 3.3, n = 57) than those travelling when captured ($\bar{X}$ weight = 152 kg, S.E. = 3.3, n = 59, $F_{1\ 114}$ = 11.2, P = 0.001), but there was no difference in the sizes of litters between the two categories ($\bar{X}$ litter size at dens = 1.93, $\bar{X}$ litter size when travelling = 1.89, $F_{1\ 118}$ = 0.17, P = 0.68).

3.3.10 Maternity dens and site fidelity

Maternity dens in spring are usually found in snow drifts along relict and extant stream and river banks and lake shores. In all cases (n = 67) the dens were situated on south or east facing drifts, on the leeward side of the prevailing winds. Two dens used in spring had been dug into the earth with a tunnel through the snow from the surface; all others were excavated entirely in snow. Overwinter snow dens appeared, however, to be located near earthen dens that were only visible in summer and autumn when the snow had melted. Eleven snow den sites were marked in spring and in each case an earthen den was found at the same site the following summer/autumn. In addition, two pregnant females that were captured in autumn at earthen dens were recaptured the following spring in snow dens within a few metres of the autumn sites. In summer and autumn, when there was little or no snow present, females were frequently found in earthen dens. Pregnant females appeared to initiate their overwinter hibernation in an earthen den, then during winter they presumably burrowed from the earthen dens into the snow drifts that formed, possibly to maintain adequate ventilation.

Earthen dens, in various stages of collapse, are common along many of the lakes and streams in the study area and are often found relatively clustered. On one southeast facing lakeshore more than 35 earthen dens were counted along 15 km of shoreline. At another lake, 19 earthen dens were visible along 6 km of east facing shoreline and another six on the banks of a small island in the lake. Dens were reused but, in our limited sample, no bear was ever observed using the same den twice. One 11 year old, presumed pregnant, female entered an earthen den in October, 1982 that had been used by a different female in October of 1980. In March, 1983 a 17 year old female and her three cubs emerged from a den that had been used the previous year by a different 16 year old female with two cubs. In March, 1984 a seven year old female with one cub was captured at a den site that had been used by an unknown family in the winter of 1980/81. Thirteen adult females were each captured in at least two separate years in spring, including one female that was handled three times. Five of the bears were captured at den sites on two occasions, with a mean distance between sites of 27 km, a median distance of 24 km, and a range of 4 km to 52 km. The remaining females were travelling to the sea ice on at least one of the years. The mean and median distance between successive spring captures for all bears, including those at dens, was approximately 34 km and the range was 3 km to 57 km. The region in the study area in which maternity dens have been found encompasses approximately 6000 km². A circle with a radius of the mean distance between a bear's successive den sites (27 km) describes an area of approximately 2300 km² or about 38% of the total denning region; a circle with radius equal to the mean distance between successive spring sightings (34 km) covers approximately 60% of the denning region. Most bears appeared to show little fidelity to an exact site on a lake shore or river bank although they did return to the inland denning region in northeastern Manitoba.

A further demonstration that bears showed lack of specific den site fidelity was obtained by comparing the distribution of dens that I observed with that recorded a decade earlier. Department of Natural Resources personnel of the Government of Manitoba flew spring aerial surveys for polar bears in fixed-wing aeroplanes over the study region between 1970 and 1976 (Stirling et al. 1977b). On these surveys all polar bears, their tracks, and potential maternity den sites were noted. The distribution of den structures seen is shown in Figure 2-6. Because they could not inspect the structures for any length of time from the air, some of the sites were probably temporary pits in the snow dug by families while walking to the sea (Ramsay and Andriashek 1986). Most of the sites seen in 1970 through 1976 were located south of or on the Owl River and more than 80% were south of Beale Creek (Table 3-12). We recorded a different pattern of den site and resting site locations during the spring work in 1980 through 1984 (Fig. 3-7). Because I used a helicopter, it was possible to inspect each site closely and determine whether it was a maternity den or a resting site. Fewer than 20% of the known maternity dens I recorded were located south of or on the Owl River and fewer than 40% south of Beale Creek. The distribution of resting sites was similar. Clearly, a distinct shift northward in the distribution of den sites appears to have occurred between the earlier and later set of surveys.

3.4 Discussion

Female polar bears inhabiting western Hudson Bay differ from their counterparts in other Canadian populations in a number of important reproductive characteristics. Interbirth intervals of two years are the most common in western Hudson Bay (39%) whereas in other populations they occur with about one-half that frequency (Ramsay and Stirling 1986a). A two-year breeding interval requires that a female wean her current litter during the spring of the cubs' second year. The high proportion of independent yearling cubs observed in the western Hudson Bay population, relative to other populations, is consistent with that observation. That these independent yearlings have survival rates similar to yearlings still with their mothers shows that a two-year breeding interval is also a viable reproductive strategy. In contrast, independent yearlings are almost totally absent (< 1%) from northern populations, suggesting that most of the females from those populations with two-year interbirth intervals lost their litters before weaning. After premature loss of a litter, a female would be available to mate again in the next breeding season (Ramsay and Stirling 1986a).

Striking differences in the size of litters also exist between northern and southern bear populations. Triplets made up 12% percent of the cub-of-the-year litters observed in spring from western Hudson Bay, and even one quadruplet litter was captured. In contrast, triplet litters are rare in other Canadian populations; occurring with a frequency of less than 1% (Stirling et al. 1980, 1984, Furnell and Schweinsburg 1984). The mean litter size of western Hudson Bay litters in spring was between 6% and 15% greater than that of any other Canadian polar bear population recorded (Stirling et al. 1976, 1980, 1984, Furnell and Schweinsburg 1984).

As would be expected from such major differences in reproductive parameters among populations, the mean natality rate of females in western Hudson Bay was 37% - 51% greater than that reported in the other populations (Stirling et al. 1976, 1980, 1984, Furnell and Schweinsburg 1984). There are two major points, however, that must be considered before natality rates calculated in this study can be compared to those of other populations. First, my calculations were made from data collected in summer/autumn whereas, in all other studies, estimates of population reproductive parameters have been determined using data collected in spring. Because cubs are known to die between spring and summer/autumn of their first year, my estimated rate of natality in western Hudson Bay was lower than if spring data had been used for the calculations. Further, simple consideration of changes in mean litter size among seasons can only give a minimum estimate of cub loss as the actual extent of loss among seasons depends on how mortality rates vary with litter size (Bunnell and Tait 1985). This is indicated by comparing different estimations of the mortality rate for western Hudson Bay cubs-of-the-year between spring and summer/autumn. Calculated from the change in mean litter size, the rate of cub mortality was 17%, whereas based on sequential captures of known families the cub mortality rate was estimated to be more than twice as great (38%).

Second, my method for the calculation of the age-specific rate of litter production was somewhat different from those used in other studies. I did not incorporate females with accompanying yearling cubs in my calculation, as was done in most of the other studies reported, because of the high proportion of females in western Hudson Bay that abandoned their cubs in the spring of their second year. Clearly, inclusion of females with yearling cubs into the numerator of our estimate would have underestimated cub production. However, even if, for purposes of comparison, I included females with yearlings in the calculation of age-specific reproductive parameters, the western Hudson Bay population still has an estimated 14% to 33% greater rate of litter production than that reported in other Canadian populations.

Over an intermediate time frame (i.e. 10^1 to 10^2 years), the natality and mortality rates of a mammalian population must balance unless the carrying capacity of the environment changes. A population with a higher natality rate and similar or lower mortality rate than another must necessarily be increasing relatively faster or declining less rapidly. There is not sufficient information at present to determine the stability or rate of growth of any Canadian polar bear population. Consequently, I cannot say whether the western Hudson Bay population is in a phase of positive growth, although that is possible. For a population to sustain long-term growth, one of two conditions, that are not mutually exclusive, must be met. If a population was reduced in the past and the causal agent was no longer in effect, the population would be expected to recover to its approximate pre-decline level. In the second case, the environment must undergo a change such that a greater number of animals can exist in a particular locale than previously. Without knowledge of historical demographics of the populations, however, differentiating between these two possibilities is not possible.

Comparison can be made between the reproductive parameters of the western Hudson Bay population and other populations that are known to be expanding to see whether clear similarities exist. In the Svalbard archipelago hunting was entirely eliminated in 1973 after several decades of heavy hunting and the polar bear population has since been increasing in size (Larsen 1985). Unfortunately, data collection methods differ between Svalbard and western Hudson Bay and direct comparison of most results is difficult. Nonetheless, the reported mean litter size of cubs-of-the-year in spring (1.83) as well as the frequency of litters of one (0.21), two (0.76), three (0.02), and four (0.01) cubs was similar to that found in western Hudson Bay and are almost identical to those reported for bears from southeastern Baffin Island (Stirling et al. 1980), a second population thought to have experienced heavy hunting pressure. Determination of interbirth intervals in the Svalbard population would allow additional comparison with other Canadian populations.

Bunnell and Tait (1981) demonstrated an inverse relationship between mean litter size in spring and latitude for 12 polar bear populations, although the populations were not identified. They imply that the increased productivity of vegetation on land in the more southern latitudes is likely the critical factor influencing litter size. Two observations run counter to this claim. First, family groups in northern Manitoba appear to spend little time in spring foraging for vegetation (Ramsay and Andriashek 1986). Even during summer and autumn when the nutritive quality of vegetation would be far superior to that found in spring, bears spend little time feeding and all lose weight, except those few with access to human refuse tips (Knudsen 1978, Lunn and Stirling 1985). Second, individual growth rates in the more southerly Canadian populations appear little different than in those bears further north, suggesting that the nutritive planes are similar in both. If food for polar bears were more abundant in western Hudson Bay than elsewhere, then one might expect this to be reflected in increased growth rates of individuals.

Limited comparative data suggest that body weights, when stratified by season, age, and reproductive class are very similar for polar bears in western Hudson Bay and the more northern Canadian populations. It follows that somatic growth rates are likewise similar between these populations. Thus, cubs that are weaned as yearlings in western Hudson Bay were no heavier than were yearling cubs in the northern populations, virtually none of which were successfully weaned.

At present there is little information on the timing and causes of mortality in young bears. A typical mammalian pattern of juvenile mortality, however, appeared to apply; mortality rates were greatest for young cubs-of-the-year and declined with age until adulthood (Caughley 1966). Although the actual mortality agents are incompletely described, they appear to preferentially affect lighter weight individuals.

Clearly, a female could increase her fitness if she were able to reduce her interbirth interval or increase the size of litter that could be weaned without sacrificing her own future reproductive effort, the survival of her post-weaning cubs to reproductive age, or their reproductive success (Altmann 1983). Unfortunately, problems associated with measuring such costs of reproduction are formidable (Bell 1980, Clutton-Brock et al. 1983). Although the life-time reproductive success of any female polar bear remains to be determined, the present data warrant consideration. Female polar bears in western Hudson Bay had a higher mean natality rate than their counterparts in other populations and their cubs appeared to have similar or even lower rates of mortality.

A related issue is whether the behavioural and developmental characteristics of cubs that are weaned as yearlings are different from cubs with a longer period of association with their mother. Increased mortality does not appear to result from early weaning in western Hudson Bay. Perhaps females from there are able to wean cubs as yearlings, not because of more abundant prey, but because the prey are more accessible to yearling cubs (Stirling and Latour 1978, Ramsay and Stirling 1982). During spring, and perhaps in winter as well, polar bears capture seals by breaking through a snow crust over seal dens and breathing holes (Stirling and Latour 1978, Smith 1980). The density and compression strength of that overlying snow might set a lower limit to the weight a polar bear can be before it can break through to capture prey. A weight limit of this form would effectively constrain cubs that weighed less to dependence on their mothers for food. The polar bears of Hudson Bay live further south than do those of any other population. One consequence is that they are limited to exploiting only annual sea ice that melts completely each summer. Snow and ice conditions on Hudson Bay may be sufficiently different from that in other Arctic marine habitats to allow successful independence of cubs at an earlier age than in more northerly regions. If this hypothesis is correct, then a principle reproductive parameter, interbirth interval, is regulated by a mechanical feature of the environment; the thickness and compression strength of snow cover.

A prediction of this hypothesis is that the force necessary to break into a subnivean seal construction should be lower in Hudson Bay than in other regions of the Arctic. Further, the compressive force that can be generated by a yearling cub should be sufficient to break into a seal lair in Hudson Bay but insufficient to do so elsewhere. To date, experimental testing of this prediction has not been carried out.

Climatic oscillations of relatively great biological significance and of intermediate frequency are a regular feature of the Arctic (Dansgaard et al. 1975, review by May 1979). Such oscillations can have profound effects on marine productivity as well as on the extent and composition of sea ice (Vibe 1967, Cushing 1982). The impact of these environmental changes on mammalian populations, including polar bears, can be profound (Dansgaard et al. 1975, Stirling et al. 1976). If early abandonment of cubs as yearlings is a polymorphic behavioural or physiological trait that occurs in even a small fraction of a polar bear population, then any environmental change that increased the probability of cub survival after abandonment could result in a rapid increase of that trait within the population. The demographic consequences of a reduction in interbirth intervals from three to two years, effected over the 15 year reproductive life of an adult female, would be pronounced. Too little is known of the dynamics of cub abandonment and cub mortality and of climatic fluctuations that may have occurred in Hudson Bay to speculate further. The scenario, however, does offer an explanation for the common existence of two year interbirth intervals in western Hudson Bay.

That nutritional status and food availability are primary constraints on reproductive performance in mammals is well documented (Sadleir 1969, McNab 1980, 1983). The long period of fasting undertaken by bears during gestation and early lactation and the concomitant period of hyperphagia prior to that fast should make the relationship between nutrition and reproduction particularly critical for them. Pregnant females, therefore, might be expected to be most stressed in years of restricted food availability (Rogers 1976, Stirling et al. 1976). The low mortality rate of adult bears and their long reproductive span suggests that females that experience nutritional stress should adopt a bet-hedging, iteroparous strategy of allocating limited resources to their own maintenance and abandon or limit any current reproductive effort. It is reasonable to assume that the amount of stores that a pregnant bear can accrue prior to fasting will dictate the reproductive partitioning of those resources (Woodside et al. 1981). This would have the effect of increasing the likelihood of an adult surviving to breed again in the future (Millar 1977, Rubenstein 1982).

Also worthy of note is the temporal pattern of weight changes experienced by female bears relative to the timing of oestrous and ovulation. A human female must attain a minimum percent body fat before menstruation can be initiated and maintained (Frisch 1984). The caloric content of that fat approximates the energetic costs of pregnancy and early lactation (Frisch and McArthur 1974). It is reasonable to suppose that such a feedback mechanism ensures that a female does not undertake the additional costs of reproduction without sufficient nutrient reserves to ensure her own survival. Similar feedback controls on fertility are well documented in other mammalian species and are regularly exploited in animal husbandry through the practice of "flushing" (Sadleir 1969, Clutton-Brock et al. 1983). Bears seemingly follow a different reproductive pattern in that oestrus occurs before the season of weight gain or maximum attained weight and, hence, prior to the assessment of fat stores available for gestation and lactation. Bears may have shifted the "decision" on whether to undertake gestation forward in time from ovulation to implantation. Rogers (1976) proposed that female bears with insufficient body reserves would fail to achieve implantation of blastocysts in the autumn and thus forego reproduction that winter.

No data are available that would support total abandonment of reproductive effort in years of lowered resource availability. Although the data on body reserves in polar bears are limited, they are consistent with the hypothesis of lowered reproductive investment in some years. In 1983, pregnant females in northeastern Manitoba were, on average, lighter in weight than in other years of the study. The mean weights of cubs in spring the next year, 1984, were markedly lighter in weight than in other years while the weights of adult females were only marginally lighter. Although it is yet too soon to detect, the 1984 cohort may be relatively absent from future demographic samples from this population because of the apparent increased mortality of cubs of lower than average weights in spring. Sizes of cub litters were no different in 1984 than in other years. Females that did give birth to cubs, therefore, did not alter the size of their litters in response to reduced nutrient stores. There was no indication that a notably high proportion of pregnant females abandoned their pregnancy in 1983-1984, although if pregnant females did not enter dens in 1983 or abandoned them prior to our spring field season in 1984, they probably would not have been detected.

Natality rate was positively correlated with age of mother, at least until 20 years of age. Why this should be so is less clear. Two general hypotheses, not necessarily exclusive, have been proposed to account for such a life-history pattern, common in birds and mammals. The first posits that parents gain experience in acquiring resources and raising offspring with each successive reproductive bout and thus improve their reproductive output with time (Curio 1983). The second proposes that a female should invest progressively more reproductive effort with age as her future reproductive potential declines (Clutton-Brock 1984). A suitable measure of reproductive costs in polar bears has, however, not been developed to allow testing either hypothesis. It is noteworthy that Kingsley et al. (1983) found that proportional changes in body weight of brown bears over winter increased with age for adult females, even as total body weight increased as well. Older females thus put both absolutely and relatively greater amounts of resources into reproduction than did younger animals.

Polar bears older than 20 years have notably lower natality rates than do younger adults and their cubs may also experience higher rates of early mortality than do cubs of younger mothers. Females without cubs found in the Manitoba denning region in spring were often old animals and they frequently displayed atypical behaviours (Ramsay and Andriashek 1986). During autumn the few solitary, and hence potentially pregnant, adult females older than 19 years weighed considerably less than would be expected from a simple extrapolation of the body weight:age relationship shown by younger adult females. All these data suggest that reproductive senescence occurs at about 20 years of age in polar bears, contrary to the suggestion of Bunnell and Tait (1981) that females maintain reproductive competency almost throughout their life. Although reproductive senescence is a well known phenomenon in human and laboratory populations, it has rarely been demonstrated in wild populations of mammals as most individuals are removed by various mortality factors before senescence occurs (Talbert 1977, Rubenstein 1983, Gouzoules et al. 1984). One consequence of large body size, however, is a lowered mortality rate of juveniles and adults allowing senescence to enter into the dynamics of a population (Calow 1977). Even so, an increase in mortality rate appears coincident with the onset of reproductive senescence; polar bears older than 20 years were proportionately less frequently found than were younger age classes. About 5% (19/376) of all females greater than four years of age are older than 20 years although such older bears comprise about 20% of all adult age classes. Functionally, therefore, female polar bears inhabiting western Hudson Bay have a reproductive span of about 15 years, from about five to 20 years of age, similar to that found in other populations (Stirling et al. 1980, 1984, Furnell and Schweinsburg 1984).

Bears, like most carnivores, have a zonary and endotheliochorial placenta (Wimsatt 1974). Characteristic of this form of placentation is that circulating levels of progesterone during pregnancy are primarily of luteal origin (Levasseur 1983, Hodges et al. 1984). Lønø (1972) noted that the corpus luteum of the post-implantation polar bear shows extensive histological change and a greater degree of vascularization than does the pre-implantation structure. Although not confirmed, it is tempting to speculate that the elevated serum progesterone levels observed in some solitary adult females in spring reflects production from newly formed corpora lutea of pregnancy. If correct, then systemic progesterone concentration rises rapidly after conception to about 5 ng/ml and stay at that level throughout the pre-implantation period. Implantation occurs in autumn (Wimsatt 1963, Lønø 1972) coinciddent with a 2-3 fold increase in serum progesterone concentration. A similar pattern in serum progesterone levels was noted in pregnant captive black bears during late summer and autumn (Foresman and Daniel 1983).

Eighty-seven percent (41/47) of solitary adult females sampled in summer and autumn showed elevated serum progesterone levels. Four of the solitary bears with anomalously low levels were in the youngest (4 years old) or oldest (>20 years old) age classes of adults, both of which are known to have relatively low rates of cub-production. The progesterone data suggest that a high proportion of the potentially pregnant bears in summer and autumn were indeed pregnant. With only two exceptions, serum progesterone levels of females with cubs and juvenile females remained low in all seasons and non-cyclic, suggesting that few, if any, bears in these age classes were pregnant. Again, this is consistent with serum progesterone levels observed for non-pregnant black bears (Foresman and Daniel 1983) and support the suggestion by Ramsay and Stirling (1986a) that pregnant females are rarely accompanied by young;

cubs are abandoned by their mothers before or soon after oestrus and mating.

Because polar bears show delayed implantation and enter dens at about the time of implantation, pregnancy can rarely be diagnosed using criteria based on foetal development (eg. foetal heartbeat detection using doppler ultrasound or rectal palpation for gravid uteri) (Follis and Spillet 1974, Barrett 1981). The presence of an ovarian bursa in bears also limits the usefulness of field laparotomy techniques for diagnosing pregnancy (Bush et al. 1978) because they require ovarian or uterine dissection that might jeopardize the female or her future reproductive performance. A single serum sample, however, obtained in July or later appears to offer a relatively simple and non-invasive means of diagnosing pregnancy in polar bears. This could be of use in future ecological studies where knowledge of the reproductive status of a free-ranging bear is desired and also to staff of zoological gardens who attempt to breed polar bears in captivity. The method may also be useful for diagnosis of pregnancyeven earlier in the year, soon after mating has occurred. Confirmation of this latter possibility will require endocrine information from bears handled immediately following the breeding season and then relocated to determine whether they had produced cubs the following year.

A rise in luteal progesterone levels in spring, soon after mating, may have nutritional ramifications. Circulating progesterone during pregnancy can affect the rate of weight gain, body composition, and control of lipogenesis in female mammals (reviewed in Hervey and Hervey 1981). Pregnant female polar bears undergo a large weight gain between the time of oestrus in spring and implantation in the autumn. The nutrient stores represented by this weight gain are the reserves required to maintain the female and her offspring as well as support cub growth during her winter fast. Elevated progesterone levels of pregnant bears during the period of weight gain may proximally mediate storage tissue composition and final weight achieved.

Polar bears appear to possess the requisite navigational skills to return to specific locations in the same season each year (Schweinsburg et al. 1982, Lentfer 1983). In Manitoba, as well, bears have been relocated at coastal sites within one km of their capture location from one or more years earlier (unpublished data). Adult females leaving their dens in spring show highly oriented movements (Ramsay and Andriashek 1986), suggesting the ability to navigate on land. Yet, adult females showed little fidelity to specific den sites. Lack of den site fidelity has been inferred for other polar bear populations (Harington 1968, Lønø 1970, Larsen 1985), but has not been confirmed through relocation of individually marked animals.

An entirely unexpected finding was the apparent shift between 1970-1976 and 1980-1984 in the centre of distribution of overwinter den sites. Inter-annual changes in the number of winter dens at other regions of concentration have usually been ascribed to variation in the pattern of local sea ice movements during the preceding summer and autumn (Harington 1968, Lønø 1970, Larsen 1985). There is no reason to believe, however, that sea ice movements or melting patterns on western Hudson Bay were notably different between the two sampling periods. The general shift in den site distribution, coupled with lack of den site fidelity, suggests that individual females do not defend territories on land. Female polar bears show no evidence of territorial behaviour at den sites, even in regions with high concentrations of bears (Hansson and Thomassen 1983).

I did not follow individual pregnant females from the time they returned ashore in summer until they chose a suitable site for an overwinter den. Hence, I do not know the behavioural patterns adopted by females searching for dens. This has never been described for polar bears. It would be of interest to determine where primiparous females locate their first den relative to their natal den site. The presence of five consecutive cohorts in the population (1980 - 1984), each of which contain a high proportion of animals captured before first reproduction, offers a good opportunity to obtain this information.

The mean duration that bears were recorded staying at den sites after emergence was 8.2 days, about two-thirds the length of post-emergence tenure recorded for undisturbed animals on Svalbard (Hansson and Thomassen 1983). My records, however, are almost certainly underestimates of the time normally spent at the opened den because I was usually unable to determine the time of emergence and abandonment.

The data suggest that adult females captured at dens in spring were, on average, heavier than were females that had already left their den and were travelling to the sea ice. Thus, a female's nutrient stores may help determine the length of tenure at a den. On Svalbard, Hansson and Thomassen (1983) noted that the female with the shortest post-emergence tenure (5 days) was also the only bear with a triplet litter and she may have been more energetically stressed than were other females. There is little food on land in spring and bears with scanty body reserves may be obliged to return to the sea ice earlier in the season than would animals with greater reserves. Although I do not know why families remain at their dens after emergence, it is not unreasonable to speculate that the period represents a time of learning, development, and acclimation for the cubs. It may offer cubs an opportunity to play in relative safety and also to allow development of the necessary motor coordination and social skills required before exposure to the harsher environment of the sea ice (Bekoff 1975, Hanssen and Thomassen 1983).

Figure 3-1. Map showing the study region.

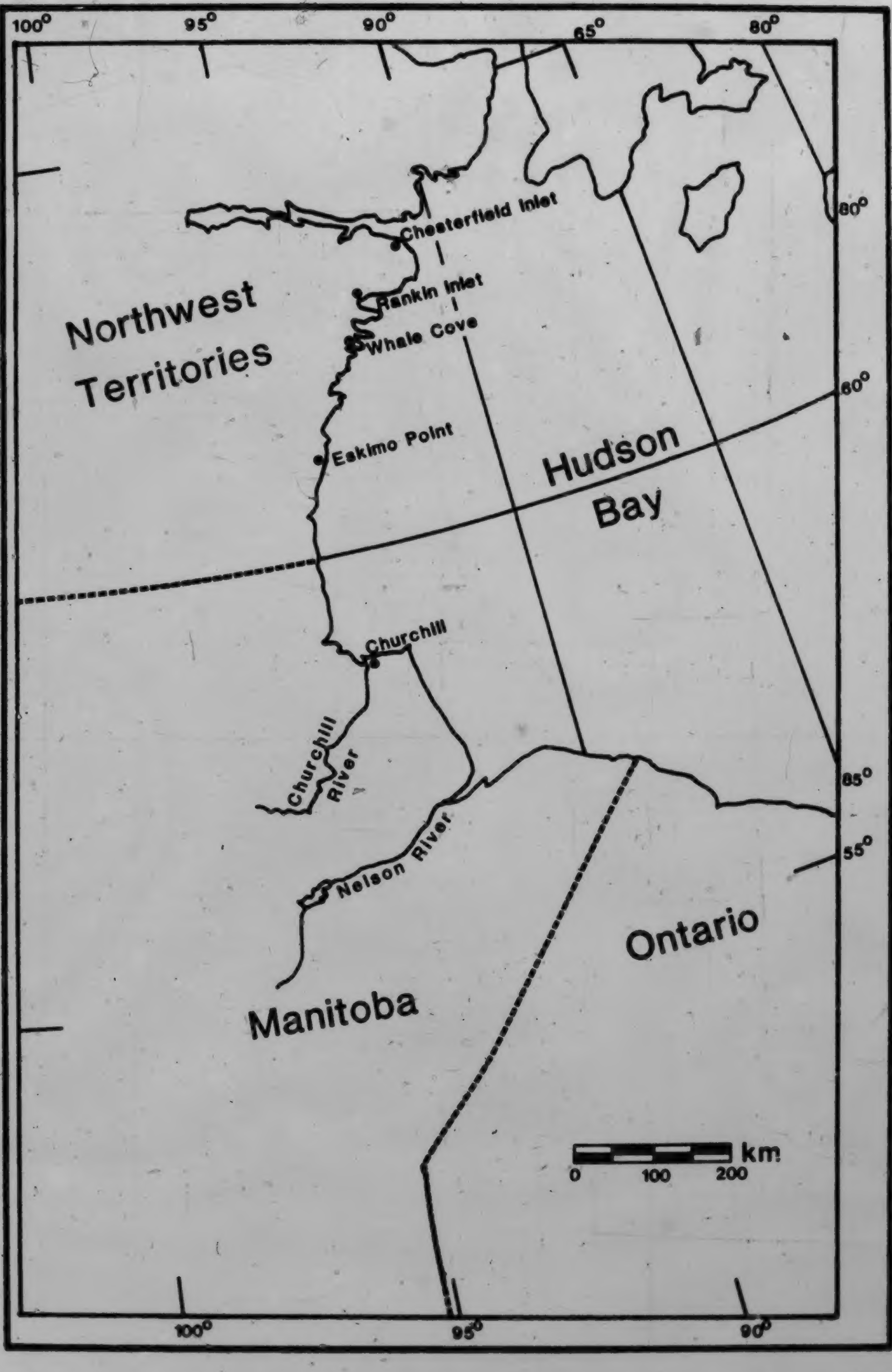
100°
95°
90°
85°
80°
80°
60°
85°
55°
Northwest Territories
Chesterfield Inlet
Rankin Inlet
Whale Cove
Eskimo Point
Hudson Bay
Churchill
Churchill River
Nelson River
Manitoba
Ontario
km
0
100
200
100°
95°
90°

Figure 3-2. Frequency of cub-of-the-year litters of differing sizes observed in spring (1980-84) and summer/autumn (1980-85) samples from northeastern Manitoba.

▦ - litters of one, ☐ - litter of two, ▨ - litters of three or four.

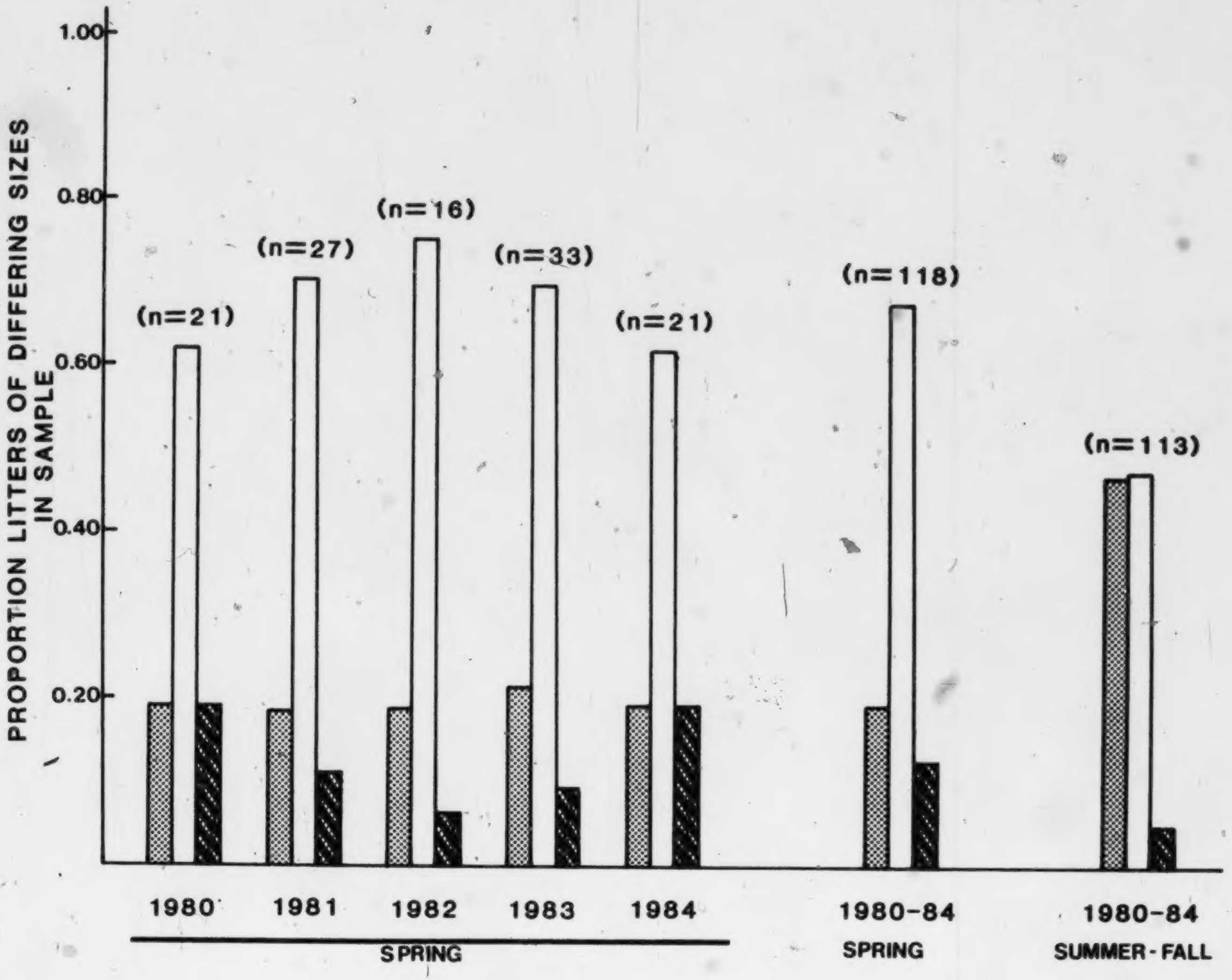
PROPORTION LITTERS OF DIFFERING SIZES IN SAMPLE
1.00
0.80
0.60
0.40
0.20
(n=21)
(n=27)
(n=16)
(n=33)
(n=21)
(n=118)
(n=113)
1980
1981
1982
1983
1984
SPRING
1980-84
SPRING
1980-84
SUMMER-FALL

Figure 3-3. Number of cubs-of-the-year lost from litters between spring and summer/autumn, 1980 - 1984 relative to the weight of adult females in spring in northeastern Manitoba. Females with single (▲), twin (●), and triplet (X) litters in spring.

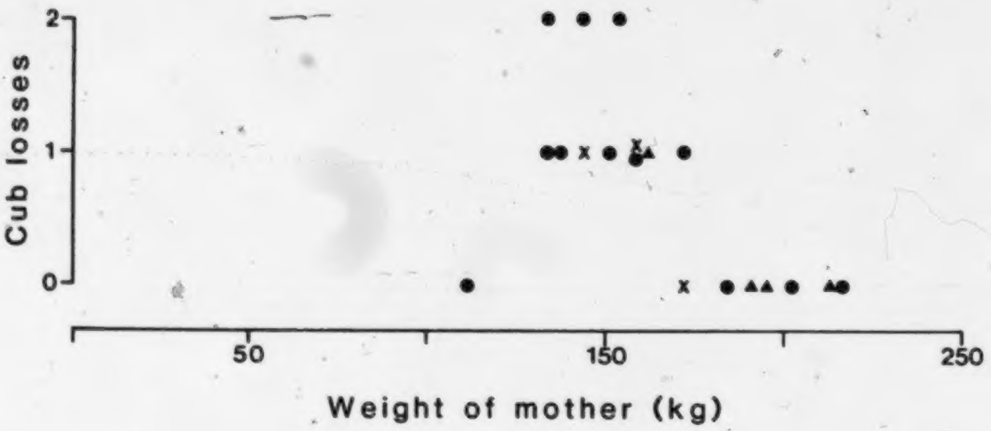
Cub losses
2
1
0
50
150
250
Weight of mother (kg)

Figure 3-4. Serum progesterone concentration (ng/ml) for female polar bears handled in the Canadian Arctic, 1982 - 1985. Bears ordered by season, age class, and reproductive category. Individual samples marked (●) except those of known-pregnant (▲) and known-breeding (◆) females. Note logarithmic scale of serum progesterone concentration.

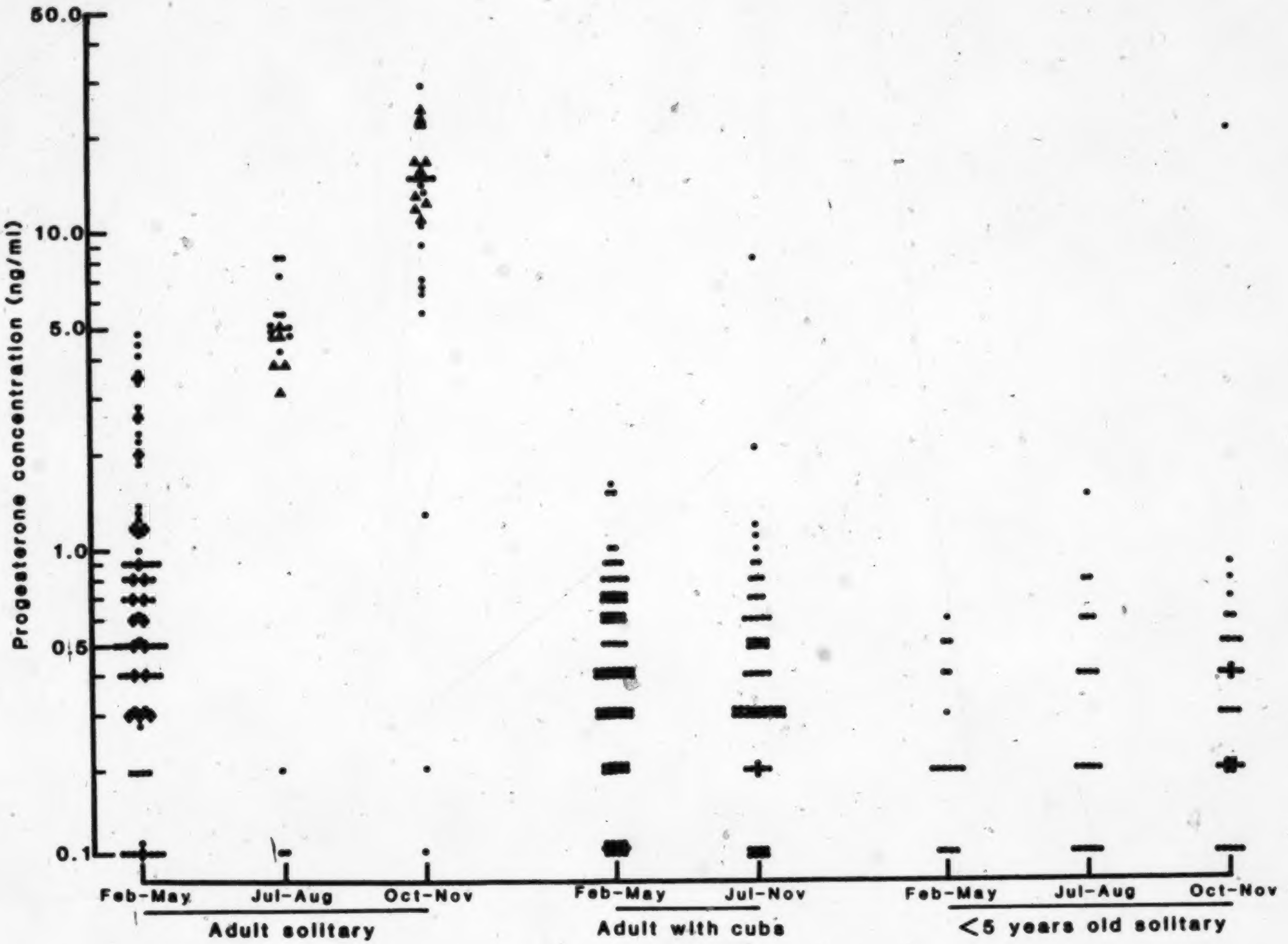
Progesterone concentration (ng/ml)
50.0
10.0
5.0
1.0
0.5
0.1
Feb-May
Jul-Aug
Oct-Nov
Adult solitary
Feb-May
Jul-Nov
Adult with cubs
Feb-May
Jul-Aug
Oct-Nov
<5 years old solitary

Figure 3-5. Serum progesterone values for solitary adult females by day of year. Span of each season of sampling is indicated by a horizontal bar. Six anomalously low values (○) were considered outliers and not used in calculating the regression, $\ln y = 0.020x - 2.94$, $r^2 = 0.79$.

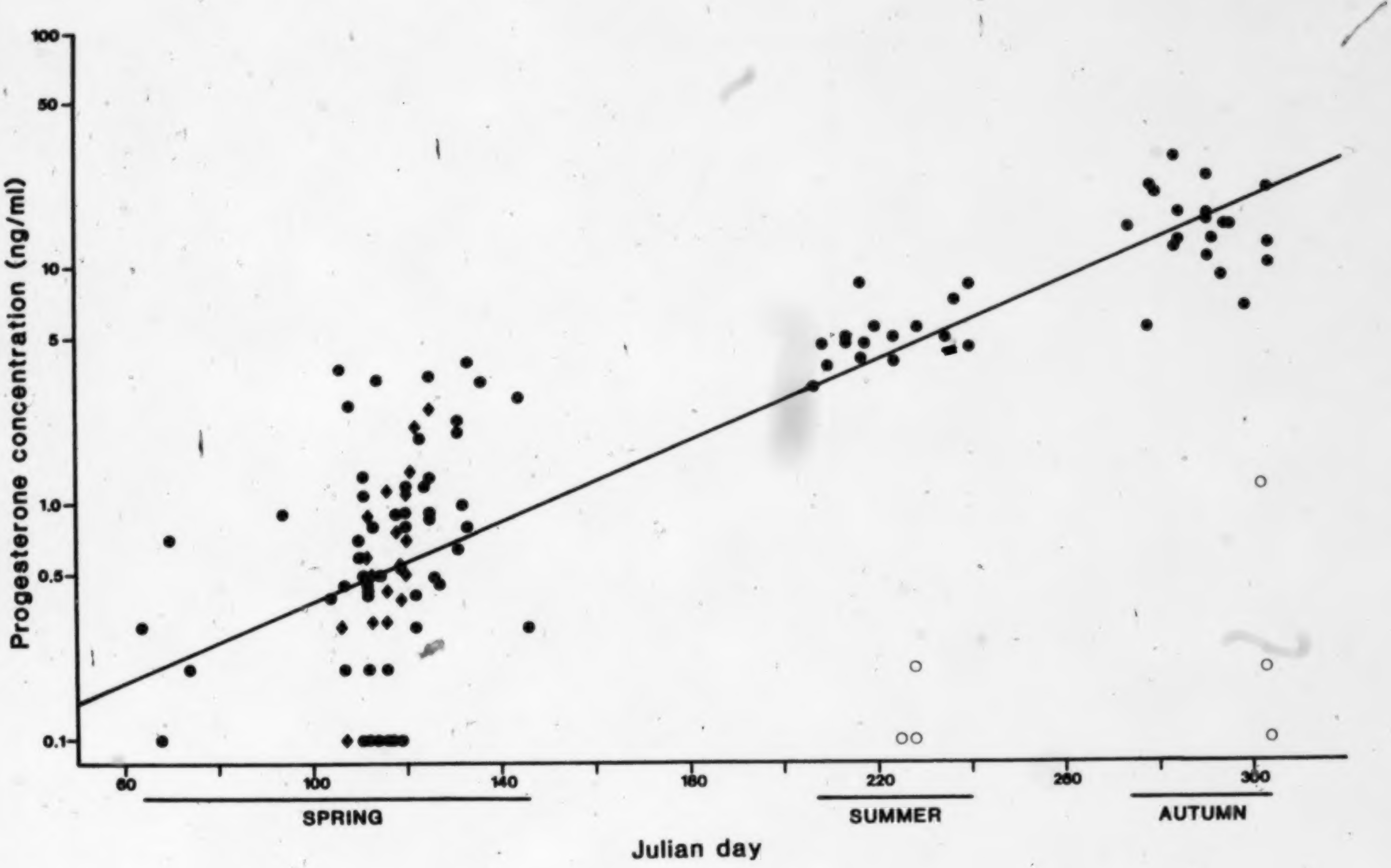
Progesterone concentration (ng/ml)
100
50
10
5
1.0
0.5
0.1
60
100
140
180
220
260
300
SPRING
SUMMER
AUTUMN
Julian day

Figure 3-6. Map of maternity denning region in northeastern Manitoba showing the location of den and resting sites of polar bear family groups sighted in February and March, 1970 - 1976. (After Stirling et al. 1977).

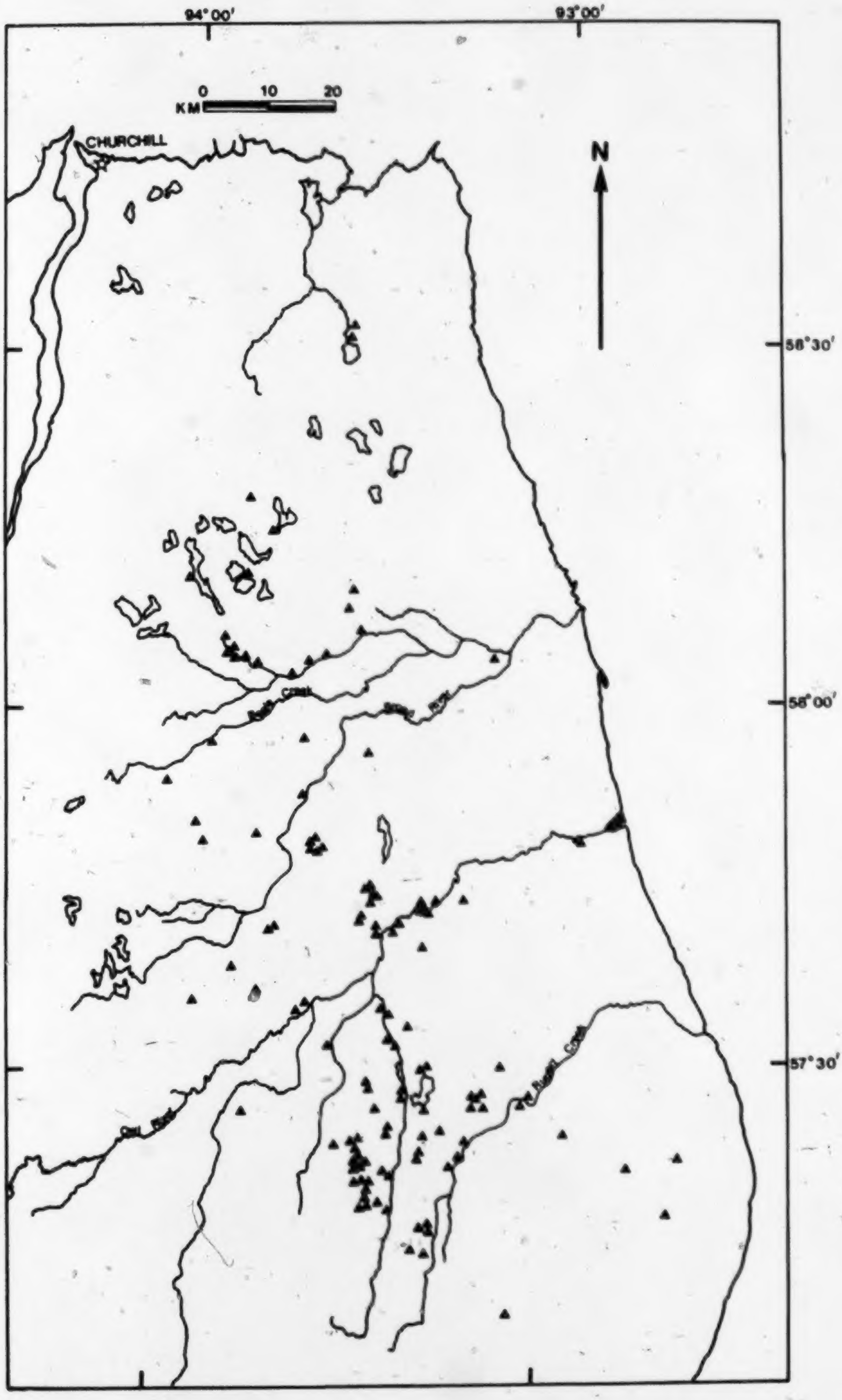
94°00′
93°00′
0 10 20
KM
CHURCHILL
N
58°30′
58°00′
57°30′
Creek
Broad River
Owl River
Rupert Creek

Figure 3-7. Map of maternity denning region in northeastern Manitoba showing the location of abandoned maternity dens (▲), occupied maternity dens (●), resting sites (◆), and travelling polar bear family groups (○) sighted in February and March, 1980 - 1984.

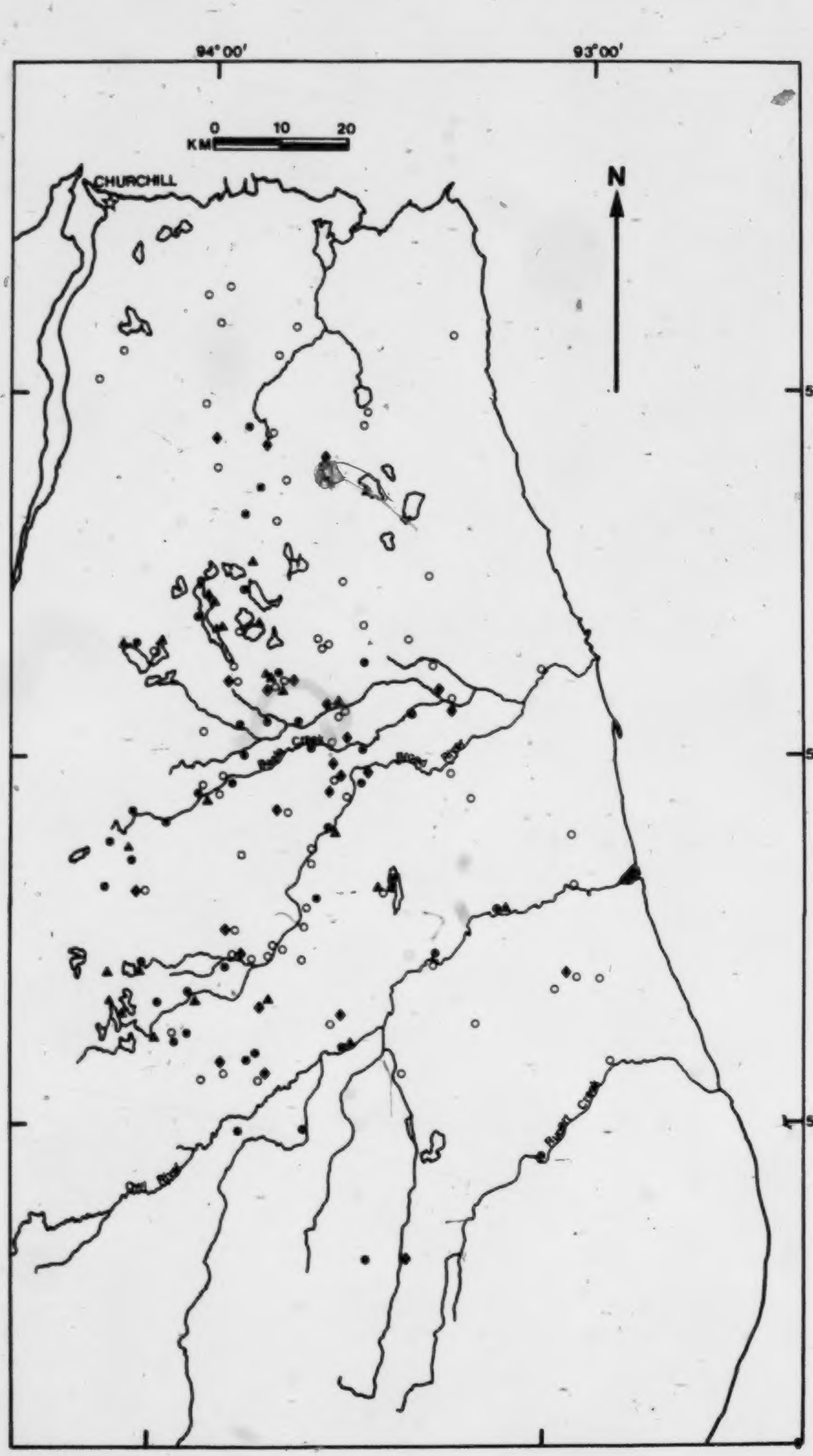
94°00'
93°00'
0 10 20
KM
CHURCHILL
N
58°30'
58°00'
57°30'
Creek
Broad
Creek
Owl River
Rupert Creek

Plate 3-1. Pregnant female polar bear in July, weighing 410 kg. Object on crown of head is a radio-transmitter glued to the fur.

Table 3-1. Age structure of female polar bears captured in Zone A1, by year in spring and summer/fall (1966-1985). Bears handled only once in any season.

year	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24+	U	total
1966		1																								1	2
1967			3							1																3	7
1968	2	2		2																						6	12
1969	2	6	3	1				1	1	1								1								3	19
1970	1	3	2	3	2			2	2		1				1											7	24
1971	6	3	5	3	4			2				2														5	30
1972	2	3		2	1	1		1																		3	13
1973	1	4	1	1	2			1						1													11
1974	5	5	1	2	1	3		1			1				1											3	23
1975	2	1	2		2	1	1	1	1	1			1													2	15
1976	7	6	2	2	1			3		1		1	1				1									2	27
1977	7	3	6	5	1	2	3	1	1		1	1	1		1	1	1	1			1					4	41
1978	3	1	3	7	1	2	1	2		1		1	1		2			1			1				1	4	31
1979	3	1	3				1		1		1			1				1			1					1	14
1980	22	5	3	1	5	1	3	4		2	2	3		5	2	4	4	3			2	1					72
1981	42	3	3	1	1	1	7	3	5	2	5	4	5	4	4	2	2	5	5			1		1			106
1982	25	15	6	3	1		2	2	1	4	1	3	3	1	3	2	4	4	2	3	2	2		1			90
1983	60	17	13	4	8	6	4	4	7	2	5	5	5	5	10	5	3	5	7	5	8	1	2	2	2		195
1984	31	11	8	3	3	4	1	7	13	1	3	3	1	4	3	2	3	2	3	2	1	2					111
1985	9		11	5	3	1	1	3	2	1	1		2		4	2	3	1				1			2		52
total	230	90	75	45	36	22	24	38	34	17	21	23	20	21	31	18	21	24	17	10	16	8	2	4	5	43	895

Table 3-2. Number of polar bears tagged in northeastern Manitoba and reported in the legal kill from communities along the Keewatin coast of Northwest Territories (1976/77 to 1982/1983 harvest, inclusive). Communities are listed from south to north.

Community	Total reported killed	Bears tagged in Manitoba in kill	Proportion tagged
Eskimo Point	202	29	0.14
Whale Cove	114	14	0.12
Rankin Inlet	117	11	0.09
Chesterfield Inlet	84	2	0.02

Table 3-3. Age structure of adult females captured in spring in the denning region of northeastern Manitoba (1980 - 1984), ordered by number of accompanying cubs-of-the-year. * indicates age class of female with quadruplet litter. No females younger than 5 years of age were seen with cubs in spring when on land.

Age of female with cubs	Age-specific mean litter size for females	Accompanying cubs			
		1 cub	2 cubs	3 or 4 cubs	None (solitary)
5	1.83	1	5		
6	1.75	2	6		
7	1.33	2	1		1
8	1.86	1	6		
9	2.00	1	2	1	
10	1.60	2	3		
11	2.00		3		1
12	2.00		6		
13	1.88	2	5	1	1
14	2.14	1	10	3	
15	2.00	1	5	1	
16*	2.40		7	3	
17	2.00	1	6	1	
18	1.78	3	5	1	
19	2.17		5	1	
20	2.17	1	3	2	1
21	1.25	3	1		1
22	1.00	2			
23	1.50	1	1		1
24					1
25					1
Total	1.93	24	79	15	8

Table 3-4. Age and litter size of cubs accompanying adult female polar bears, by age class, handled in northeastern Manitoba in summer and autumn (Aug - Nov), 1966 - 1985.

Age of female	Total no. in each age class	No. with cubs	Cubs-of-the-year			Yearlings		
			1	2	3	1	2	3
2	73	0						
3	46	0						
4	38	2	2					
5	16	8	6	1		1		
6	15	9	4	3		2		
7	34	21	7	7		1	6	
8	28	19	8	5		3	3	
9	13	10	4	6				
10	17	13	5	3		2	3	
11	17	13	3	4	2		4	
12	12	9	5	1	1	2		
13	12	12	3	4	1	1	2	1
14	16	14	6	5		2		1
15	12	10	2	3	2	2	1	
16	12	7	1	5		1		
17	15	11	3	5	1	1	1	
18	9	9		4	1		4	
19	3	1	1					
20	8	7		5			2	
21	2	0						
23	1	0						
24	1	0						
25	1	0						
30	1	0						
Total	402	175	60	61	8	18	26	2
Proportion of total			0.47	0.47	0.06	0.39	0.57	0.04

Table 3-5. Age specific rate of litter production, mean litter size, and natality rate for female polar bears calculated using females with cubs-of-the-year in northeastern Manitoba captured in summer and autumn (August - November), 1966 - 1985. Methods of calculation of reproductive parameters given in text. Summary statistics for combined age groups listed at bottom of table. Sample sizes in parentheses.

Age of female in year cub born	Age-specific rate of litter production	Age-specific mean litter size	Age-specific natality rate
3	0.000 (46)	0.00 (0)	0.000
4	0.053 (38)	1.00 (2)	0.057
5	0.438 (16)	1.14 (7)	0.499
6	0.467 (15)	1.43 (7)	0.668
7	0.412 (34)	1.50 (14)	0.618
8	0.464 (28)	1.38 (13)	0.640
9	0.769 (13)	1.60 (10)	1.230
10	0.471 (17)	1.38 (8)	0.650
11	0.529 (17)	1.89 (9)	1.000
12	0.583 (12)	1.43 (7)	0.834
13	0.667 (12)	1.75 (8)	1.167
14	0.688 (16)	1.45 (11)	0.998
15	0.583 (12)	2.00 (7)	1.166
16	0.500 (12)	1.83 (6)	0.915
17	0.600 (15)	1.78 (9)	1.068
18	0.556 (9)	2.20 (5)	1.223
19	0.333 (3)	1.00 (1)	0.333
20	0.625 (8)	2.00 (5)	1.250
20+	0.000 (6)	0.00 (0)	0.000
5 - 9	0.483 (106)	1.43 (51)	0.69
10 - 14	0.581 (74)	1.58 (43)	0.92
15 - 19	0.549 (51)	1.89 (28)	1.04
20 - 24	0.417 (12)	2.00 (5)	0.83
5 - 20	0.531 (239)	1.61 (127)	0.86

Table 3-6. Maximum interbirth intervals (years) and the minimum mean natality rate for female polar bears captured on two or more occasions with cubs of different litters in northeastern Manitoba (1966 - 1985). Proportion of cycles for each time interval in parentheses.

No. of cycles for each interbirth interval						Total no. of cycles observed	Total no. of bear years	Total no. of cubs	Natality rate
1	2	3	4	5	6				
2	26	21	12	2	3	66	193	123	0.637
(.03)	(.39)	(.32)	(.18)	(.03)	(.05)				

Table 3-7. Number of yearling cubs captured in northeastern Manitoba during summer - autumn (August - November), 1966 - 1984, by sex and weaning status. Proportion of total number of cubs that were alone shown in parentheses.

Weaning status of yearlings at capture	Sex		
	female	male	Both
with mother	37	39	76
alone	49	44	93
Total	86 (0.57)	83 (0.53)	169 (0.55)

Table 3-8. Mean calculated weights (kg) ± 1 S.E. of female polar bears older than four years captured in western Hudson Bay during the on land period, but not captured in the vicinity of the town of Churchill or its garbage dump, (1970 - 1984). Sample sizes in parentheses. Arrows indicate the temporal changes in reproductive classes, assuming no losses of litters occurred between seasons.

Accompanying bears	Summer (Jul - Aug)		Autumn (Oct - Nov)		Spring (Feb - Mar)
None	249 ± 11 (22)	→	230 ± 7 (40)	→ ↘	199 ± 10 (6)
Cubs-of-the-year	190 ± 5 (46)	→	152 ± 4 (37)		159 ± 2 (118)
Yearling cubs	191 ± 6 (16)	→	170 ± 6 (17)		

Table 3-9. Proportion of bears in northeastern Manitoba initially handled as cubs-of-the-year (1966-1984) and recaptured at least one year later (1967 - 1985), as a function of litter size or sex and season. Differences in totals result from sex being unknown for some animals.

Size of litter or sex of cubs when initially handled	Proportion recaptured (cubs initially handled in spring)	Proportion recaptured (cubs initially handled in summer/autumn)
1	3/21 = 0.14	14/54 = 0.26
2	11/134 = 0.08	19/94 = 0.20
3 or 4	5/34 = 0.15	9/21 = 0.43
Total	19/189 = 0.10	42/169 = 0.25
female	7/93 = 0.08	23/95 = 0.24
male	12/96 = 0.13	19/69 = 0.28

Table 3-10. Mean weights (kg) ± S.E., by litter size and sex in year of capture, of cubs-of-the-year in spring (February - March) in northeastern Manitoba. Sample sizes in parentheses.

Litter size or sex	Year					
	1980	1981	1982	1983	1984	1980 - 1984
1 cub	14.6 ± 3.8 (4)	15.5 ± 1.6 (6)	11.8 ± 1.6 (3)	14.9 ± 1.3 (7)	12.0 ± 3.0 (3)	14.2 ± 0.9 (23)
2 cubs	10.6 ± 0.4 (26)	12.2 ± 0.3 (34)	11.7 ± 0.6 (24)	11.2 ± 0.4 (46)	9.3 ± 0.4 (22)	11.1 ± 0.2 (152)
3 or 4 cubs	8.5 ± 0.8 (9)	9.6 ± 1.2 (9)	6.4 ± 1.1 (4)	8.7 ± 0.9 (9)	7.7 ± 1.0 (9)	8.4 ± 0.5 (40)
Total	10.6 ± 0.5 (39)	12.2 ± 0.4 (49)	11.0 ± 0.6 (31)	11.2 ± 0.4 (62)	9.1 ± 0.5 (34)	10.9 ± 0.2 (215)
Females	9.3 ± 0.5 (17)	12.2 ± 0.7 (26)	10.9 ± 0.7 (14)	10.7 ± 0.5 (32)	8.5 ± 0.8 (17)	10.5 ± 0.3 (106)
Males	11.5 ± 0.8 (22)	12.1 ± 0.5 (23)	11.2 ± 0.9 (17)	11.7 ± 0.6 (30)	9.7 ± 0.5 (17)	11.4 ± 0.3 (109)

Table 3-11. Mean body weights (kg) ± S.E., by season and sex, of cubs-of-the-year and yearling cubs in northeastern Manitoba. Sample sizes in parentheses.

Age of cub and sex	Season	
	Summer	Autumn
Cub-of-the-year Female	53.4 ± 2.2 (38)	42.0 ± 1.6 (36)
Cub-of-the-year Male	58.9 ± 3.0 (30)	48.1 ± 3.2 (23)
Cub-of-the-year Total	55.8 ± 1.8 (68)	44.4 ± 1.6 (59)
Yearling cub Female	119.0 ± 7.0 (14)	91.8 ± 5.4 (33)
Yearling cub Male	133.4 ± 9.0 (14)	116.8 ±3.6 (31)
Yearling cub Total	126.2 ± 5.8 (28)	103.9 ±3.6 (64)

Table 3-12. Number of potential maternity den sites (1970 - 1976 and 1980 - 1984) and captured females (1980 - 1984) located in spring in northeastern Manitoba. Proportions of total in each row in parentheses. Symbols used as in Figures 3-6 and 3-7.

Years	Sites	Locations			
		Whole study region	South of or on Owl River	Between Beale Creek and Owl River	North of or on Beale Creek
1970 - 76 (Figure 3-6)	possible maternity sites (▲)	119	75 (0.63)	24 (0.20)	20 (0.17)
1980 - 84 (Figure 3-7)	females at maternity sites (●)	42	7 (0.17)	16 (0.38)	19 (0.45)
	abandoned maternity sites (▲)	25	2 (0.08)	10 (0.40)	13 (0.52)
	resting sites (◆)	23	2 (0.09)	12 (0.52)	9 (0.39)
	Total all sites	90	11 (0.12)	38 (0.42)	41 (0.46)
	females travelling (○)	73	8 (0.11)	26 (0.36)	39 (0.53)

3.5 Literature cited

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4. ON THE MATING SYSTEM OF POLAR BEARS[2]

4.1 Introduction

Recent studies have contributed considerably to understanding the ecological underpinnings of particular mammalian reproductive behaviours and have generated the data necessary for constructing theoretical models of reproductive strategies (e.g. Weir and Rowlands 1973, Bekoff et al. 1981, Irons 1983). Most of these models have been developed for relatively social species. Where behavioural studies of solitary species have been made, few data are available concerning behaviours associated directly with breeding.

Bears (Ursidae) are a case in point. Although conspicuous members of their communities, the breeding behaviour of bears is not well known. Questions regarding the control of oestrus in females, the degree to which females choose mates, courtship behaviours, male access to oestrous females, intrasexual male fighting, degree of polygyny, and the probability of conception for any one copulation are wholly or partially unanswered.

Polar bears (*Ursus maritimus*) live in a sufficiently different habitat from other bears that they might be expected to differ with regard to behaviours associated with breeding. The major difference in the environment of polar bears from that of their congenerics is in the degree of uncertainty associated with the distribution and abundance of resources. This uncertainty is due primarily to the high degree of seasonal and annual variability of productivity in the arctic marine habitats where polar bears hunt (Nemoto and Harrison 1981). Ringed seals (*Phoca hispida*) and, to a lesser degree, bearded seals (*Erignathus barbatus*) are the predominant prey of polar bears. Their seasonal and local abundance, as well as their vulnerability to polar bear predation, is strongly influenced by sea ice conditions (Stirling and Archibald 1977, Smith and Stirling 1978). Sea ice, in turn, is affected markedly by winds, currents, and climatic conditions (Jacobs and Newell 1979, Catchpole and Faurer 1983). Thus, although long-term average sea-ice conditions and productivity may be predictable, local conditions are unpredictable both within and among seasons. Both male and female polar bears may move considerable distances in some years to locate regions of seal abundance (Lentfer 1983, Schweinsburg et al. 1982), regions which can also vary among years. Perhaps in consequence, male and female polar bears do not maintain relatively discrete home ranges as described for brown (*U. arctos*) and black (*U. americanus*) bears (Amstrup and Beecham 1976, Lindzey and Meslow 1977, Reynolds and Beecham 1980, Young and Ruff 1982, Servheen 1983), and the distribution of female polar bears available for breeding is unpredictable among years.

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Like other ursids, female polar bears have low natality rates and high cub survival to the age of weaning. They give birth for the first time at a relatively advanced age, litter sizes are small, and interbirth intervals are a minimum of two years, and more usually three, if cubs are weaned successfully (Herrero 1978, Bunnell and Tait 1981, Ramsay and Stirling 1982). The breeding season for polar bears has not been well defined, but is thought to extend from March through May (Lønø 1970). During this period, males have been observed in agonistic intrasexual encounters (Lønø 1970, Latour 1981). Although copulation has not been described in the literature, males have been observed in spring interacting with females and presumably engaged in courtship (Lønø 1970). In contrast, agonistic intersexual interactions have been noted outside of the purported breeding season, and females with accompanying cubs generally avoid associating with adult males (Stirling 1974, Lunn and Stenhouse 1985, Taylor et al. 1985).

I did not observe the breeding behaviour of polar bears, except incidentally during studies directed to other objectives. However, data were collected on patterns of inter-

and intrasexual associations during the breeding and non-breeding seasons and on the prevalence of scarring, wounding, and tooth breakage by age and sex class. I believe these data are directly related to breeding behaviour and offer insight into the nature of the mating system of polar bears.

4.2 Study area and methods

All data were collected from polar bears captured alive, between 1966 and 1985, during studies on their ecology and population dynamics. Within Canada, polar bears are distributed in a number of relatively discrete populations (Fig. 4-1) (Stirling et al. 1975, 1977, 1980, 1984, Schweinsburg et al. 1982, Furnell and Schweinsburg 1984). The most extensively sampled populations have been those in western Hudson Bay (A1), southeastern Baffin Island (D), High and Low Canadian Arctic archipelago (E and F respectively), and the eastern Beaufort Sea (H).

Bears were captured using standard chemical immobilizing methods (Lentfer 1968, Larsen 1971). Most animals were located during search operations from a helicopter and subsequently shot with darts containing immobilizing drugs. Each bear handled was marked with an ear tag and tattoo with an identifying number. In addition, a temporary number was dyed on the pelage of the back to facilitate identification from the air during the season of capture. A vestigial premolar tooth was extracted for age determination, using counts of incremental lines in cementum (Stirling et al. 1977), and the sex and reproductive status of each bear was determined. Adult females ($\geq$ 5 years of age) were classified as solitary or accompanied by cubs-of-the-year, yearling-cubs, two-year-old cubs, or adult males. Adult males ($\geq$ 5 years of age) were classified as solitary or accompanying an adult female.

To determine intersexual relationships, bears were classified by association relative to others only at the time of capture and usually not on any subsequent resightings during the same season. In any one season, most bears were sighted only at their time of capture and the few resightings made were usually within a few days of capture when the possible effects of chemical immobilization and capture stress might have resulted in short-term, atypical behaviours. I assumed, however, that capture and handling of bears had no long-term effects on any of the reproductive parameters measured (Ramsay and Stirling, 1986). An adult male and female were considered to be associated if they were within about 100 m of each other when first sighted. It was usually obvious from their tracks in snow if they were travelling together. Adult bears in association when sighted were most often captured together, but if both could not be captured then the males were allowed to escape. Non-captured bears consorting with adult females were assumed to be adult males unless, based on body size, they were clearly subadults.

Stirling et al. (1981) described the spring distribution of polar bears in the eastern Beaufort Sea, between 1971 and 1977, relative to differing sea ice habitats. During polar bear capture operations using helicopters they recorded the number of km flown over each type of ice habitat and the number of bears captured on each. Seven varieties of sea ice were recognized, three of which made up 88% of the total distance surveyed during helicopter search operations (65,658 km/74,332 km). The remaining 12% of the total distance flown was over the other four recognized ice types. Ninety-seven percent (441/454) of the adult bears seen were on the three most common ice types. Survey methodologies are given in Stirling et al. (1981). The three common ice habitat types were:

Type 1. Stable landfast ice with snow drifted pressure ridges.

Type 3. The floe edge, with wide leads, including areas of less than 7/8 ice cover.

Type 4. Active ice regions of more than 7/8 ice cover.

Using the data of Stirling et al. (1981) I have calculated indices of relative polar bear abundance on each of the three most common ice types as the quotient of the proportion of each adult reproductive class found on a particular ice type divided by the proportion of search distance spent on that ice type. An index value of 1.0 for an ice type would indicate that the bears of the reproductive class considered were found on that ice type in proportion to its frequency of occurrence. Index values less than 1.0 would indicate lower than proportional abundance on that ice type and values greater than unity would reflect the opposite.

Indices chosen as measures of tooth wear, tooth breakage, scarring, and wounding were qualitative and, necessarily, arbitrary. The incisors, primarily used in feeding, were used to measure tooth wear because they were easily examined and, hence, rapidly evaluated in the field. Three wear categories were established, modified after Rausch (1961), based on the degree of wear on the occlusal surfaces. Teeth with no, or only slight, wear were classified in the first category; teeth with slightly more wear to those in which the dentine was just exposed in the second category; and those with extensive wear into the dentine layer in the third. The canine teeth, as weapons, were chosen as indicators of tooth breakage. Any bear that had at least one canine tooth with more than 1 cm, or approximately one third of the crown length, broken from the tip, was classed as showing tooth breakage; all others were classified as being without breakage.

In two populations, western Hudson Bay and eastern Beaufort Sea, bears were examined for both scars and fresh wounds, especially on the head, neck, shoulders, forelegs, hips, and hindlegs. Only two categories, presence or absence, were scored. Classification to scarring category was determined by whether a bear had more or less than about 25 cm^2 total area of scar tissue. All fresh or open body wounds, of any size, were recorded and bears were classified by their presence or absence, regardless of their severity or extent.

Polar bears were captured primarily during March through May in the Canadian Arctic north of 60° N latitude (populations D, E, F, H; Fig. 4-1), because favourable ice and weather conditions then resulted in the greatest catch-per-unit-effort (Stirling et al. 1980). During that season, females with cubs-of-the-year were out of their dens and on the sea ice, available for capture along with all other age and sex classes. Fewer bears were captured during June through November and most of the effort then was concentrated in July and August.

The seasonal timing of capture was different in western Hudson Bay where each summer the sea ice melted and all bears were forced ashore (Stirling et al. 1977). Most capture effort was expended from late July to mid-November when the entire population could be sampled easily while on land. Spring capture operations (February - March) in western Hudson Bay were primarily conducted in the inland denning region of Manitoba, where there were only adult females and their newborn cubs-of-the-year leaving their overwinter dens (Jonkel et al. 1972, Stirling et al. 1977, Ramsay and Andriashek 1986).

Females from western Hudson Bay had a higher mean natality rate and a shorter breeding interval than bears in more northerly populations (Ramsay and Stirling 1982). Because of the seasonal differences in sampling and the differences in reproductive parameters between western Hudson Bay and the more northerly populations, data from western Hudson Bay were considered separately, except where noted.

Analysis of frequency data was carried out using the log-likelihood ratio test (G-test) or Fisher's exact test (Sokal and Rohlf 1981). Comparisons of age structure and tooth wear among strata of bears were made using the nonparametric Mann-Whitney test (Conover 1980). All statistical calculations were carried out with BMDP (Department of Biomathematics, The University of California, Los Angeles) statistical software.

4.3 Results

4.3.1 Females

In the four most northerly Canadian polar bear populations studied, (populations D, E, F, H) cubs normally accompanied their mother until, at least, the spring of their third year, when they were about 2.5 years old. Of 26 adult females from the four northerly populations for which an interbirth interval was known, only five (19%) had cubs more frequently than once every three years, while 14 (54%) had successive litters of cubs three years apart. An interbirth interval of two years requires that the earlier litter be weaned at about 1.5 years as yearling cubs. Since independent yearling cubs were rarely observed in the northern populations, females with interbirth intervals of less than three years probably lost or prematurely abandoned their earlier litter of cubs before they could achieve independence. Of 210 yearling cubs captured in the northerly populations, only seven were independent. None of these seven were ever subsequently recaptured or killed by hunters, suggesting that their survival rate was low. In contrast, 42% of the two-year-olds captured (95/225) were independent and the rate at which they were recaptured or killed by hunters (0.34), was not significantly different from that of two-year-olds that were with their mothers when first caught (0.29) ($G = 0.51$, d.f. = 1, $P = 0.48$).

During the spring breeding season, adult females without cubs were much more likely to be found in proximity to adult males than were adult females with accompanying cubs (Table 4-1). Assuming that adult males associated with adult females to obtain breeding opportunities, then adult females without cubs were apparently courted with considerably higher frequency than those with cubs. This is consistent with the data on interbirth intervals; few females had cubs more frequently than every three years, hence females with cubs less than two years old presumably rarely came into oestrus. The frequency of association with males was similar and low for all females outside the breeding season and for females within the breeding season that were with cubs of any age ($G = 0.31$, d.f. = 1, $P = 0.58$). The most common interbirth interval recorded was three years, suggesting that many cubs were weaned when they were two-years old. Yet females accompanied by two-year-old cubs in spring were infrequently observed with accompanying adult males suggesting that cubs were abandoned before the mothers associated with males or soon after a male approached.

Several other data support the hypothesis of abandonment of two-year-old cubs by females before or soon after they breed. Twenty-two females, handled in March through May, were known to have bred in the season of capture because they were subsequently recaptured with cubs that must have been conceived then. Adult males were with seven of these females when captured. Twelve of the females were handled in May when none had accompanying cubs, whereas five of the ten bears handled in March and April were with two-year-old cubs and one was with cubs-of-the-year. Additionally, only three of 77 females captured with two-year-old cubs were also with an accompanying male (Table 4-1), yet two of these three females were among those known to have successfully conceived in the year sampled. In contrast, of the remaining 74 females that were captured in spring with two-year-old cubs but without accompanying males, only three were known to have conceived, a difference that is significant (Fisher Exact Test, $P = 0.01$).

For all Canadian populations, 26 known-pregnant bears were captured from June through October. Only one of these was with two-year-old cubs and none of the others were with cubs of any age. The only known-pregnant female with cubs was captured in July. She had also been captured in each of the two previous years with the same cubs, as cubs-of-the-year and yearlings respectively. During April, prior to their July handling, one of those two-year-old cubs was captured alone. The cubs may, therefore, have been abandoned by their mother when she was in oestrus, or driven off by a consorting male, and then rejoined her after she had bred.

One female from the northern populations captured in spring with accompanying cubs-of-the-year was known to have also bred in that year. In western Hudson Bay, one female of the 119 that were captured in spring with cubs-of-the-year, was known to have bred in the same year that she gave birth. Therefore, at least some females that lose their pre-weaning age cubs prior to or during the breeding season are able to come into oestrus and breed again. One measure of the extent of early cub loss and the opportunity for re-breeding was obtained by following individual females and their litters through time. From the northern Canadian populations that were sampled in spring, 25 adult females with cubs-of-the-year were recaptured one year later when the cubs would have been yearlings. Mean size of litters in the sample dropped from 1.7 for cubs-of-the-year to 1.1 for yearling cubs. About one-quarter (5/17 = 0.29) of the litters of two lost one cub between their first and second years and about one-quarter (4/17 = 0.24) lost both cubs, but only 1/8 (0.13) of the single-cub litters were lost. Therefore, five females lost their whole litter and could have bred in the same year as they gave birth if the losses were before or during the breeding season. There was no significant difference in the proportion of female (0.31) and male (0.36) cubs lost (G = 0.10, d.f. = 1, P = 0.75). Cub mortality soon after emergence from the winter den would not have been detected in these high-latitude studies as we only handled bears there on the sea ice, away from the maternity denning regions.

Families in western Hudson Bay during spring were captured at or near their overwinter maternity dens and before they had migrated to the sea ice. Twenty-one females with cubs-of-the-year were captured in spring and then recaptured in summer and autumn of the same year. The mean litter size of these families in spring was 1.9, but by summer/autumn it had declined to 1.2. The proportion of females with twin litters that lost both cubs (3/13 = 0.23) was similar to that in the more northerly populations and the proportion of litters in which all cubs were lost was not significantly different between the northern populations (5/25 = 0.20) and western Hudson Bay (4/21 = 0.19) (G = 0.01, d.f. = 1, P = 0.94). Again, there was no significant difference in the proportion of female (0.35) and male (0.38) cubs that disappeared (G = 0.032, d.f. = 1, P = 0.86). Although families in western Hudson Bay were handled in spring at an earlier stage of their development than in more northerly populations, there was no evidence of a greater propensity for females to lose whole litters or to breed again. Eight solitary adult females, not accompanied by cubs, were also captured in the

Manitoba denning region between 1980 and 1984. Two were captured at den sites, each with a single dead cub. One of these bears had unusually elevated blood urea levels at the time of capture, possibly indicating prolonged starvation with associated catabolism of body protein, and subsequently died near her den without returning to the sea ice. Some of the other solitary bears might also have lost their cubs and would therefore have had the opportunity of breeding again later in the spring of the same year. One of these eight did breed later the same spring as she was recaptured the following year with cubs-of-the-year. The solitary females were, however, significantly older than females with cubs-of-the-year and some were likely reproductively senescent (Ramsay and Andriashek 1986).

During capture operations, most bears that were sighted were captured. I found little evidence to suggest that certain age or sex classes were consistently under- or over-sampled. Therefore, I assume that the bears handled were representative of the population during the sampling periods. More than 30% of the solitary females (Table 4-1) and bears known to have been in oestrus were in association with males at the time of their capture in spring. Such a high percentage of inter-sexual associations seen in a randomly sighted sample of animals suggests that individual females are available to breed with males for extended periods of time. There are two possibilities to account for these data: individual females could consort with individual males for a considerable length of time, or they could breed with more than one male in succession in a single season. Without continuous observations on individual breeding bears, these alternatives cannot be clearly distinguished. We did obtain a few opportunistic observations of male tenure with females during the breeding season. One marked female without cubs was observed in association with the same marked male on three occasions during a nine day period, and a second female was periodically seen with another marked male over an eight day period. On several occasions, male - female consorting pairs were encountered along the coastlines of both the High Arctic Islands and southeastern Baffin Island. In each of these cases, tracks in snow indicated that the pairs had been together for several days and had mated several times. Some of the males appeared to have herded the females and directed their movements, usually into small bays or onto hillsides, away from the productive areas of sea ice where most other bears were hunting seals. Although such sequestering was not possible in all habitats or areas, it frequently appeared that males attempted to isolate individual oestrous females away from areas where they might encounter other males.

Although most consorting females were only with a single male when captured in spring, almost 8% (7/91) of them were associated with more than one adult male. In these cases, the females were probably in consort with one male and the others were incipient challengers of the consorting male or bears that had just been displaced as consort of the female. Two females were each seen on two occasions in the same spring with different adult males. Both multi-male consorts and females associated with two or more single males in the same season suggests that females may mate with more than one male. Without supporting data, however, such observations do not preclude the possibility that oestrous females only copulated with one of the males in a multi-male group.

4.3.2 Males

In order to obtain breeding opportunities males must locate and associate with adult females. Yet, few of the adult males captured were seen in association with adult females, of any reproductive status, during the breeding season (Table 4-1). Only about 13% of captured adult males were associated with adult females, whereas 32% of adult females without cubs were associated with adult males. Furthermore, 14 of the 80 adult males captured with adult females in spring were also with one to four other males. Therefore, males that were accompanying females may not have had equal opportunity for breeding. Admittedly, the number of males captured with females was biased slightly downward because some males escaped when females they were accompanying were immobilized. Working from a helicopter precluded obtaining behavioural information on hierarchical relationships among males and their frequency of copulation with females. Adult males with adult females were, on average, older (median age = 10.5 years, range of ages = 5 - 24 years, *n* = 74) than adult males that were solitary during the breeding season (median age = 8.0 years, range of ages = 5 - 25 years, *n* = 540), a difference that is significant (Mann-Whitney U = 15,675, *P* = 0.003).

Adult polar bears were not found with equal frequency of occurrence in all ice habitat types, nor were distributions similar among most reproductive classes (Table 4-2). Type 3 ice habitat had the greatest overall density of bears while Type 1 had the least. Over all three ice habitats the relative indices of abundance for adult males and solitary adult females were similar, whereas little concordance in relative abundance was found between any other pair of reproductive classes.

Table 4-3 summarizes the observed prevalence of tooth wear, tooth breakage, wounding, and scarring for adults of both sexes. Males were significantly more likely than females to have broken canines (G = 22.2, d.f. = 1, $P < 0.001$), wounds (G = 23.8, d.f. = 1, $P < 0.001$), and scars (G = 97.3, d.f. = 1, $P < 0.001$). By contrast, the degree of tooth wear was similar for both sexes. There was no significant difference between females and males in the median ages that were assigned to tooth wear categories one (females = 7 yr, *n* = 83; males = 7 yr, *n* = 65; Mann-Whitney U = 2945, *P* = 0.33) and three (females = 20 yr, *n* = 20; males = 20 yr, *n* = 15; Mann-Whitney U = 168, *P* = 0.55). Males assigned to tooth wear category two, however, were significantly younger than females assigned to the same category (females = 15 yr, *n* = 83; males = 13 yr, *n* = 63; Mann-Whitney U = 3250, *P* = 0.01).

Although I have no quantitative assessment of the severity of injuries on individual bears, our subjective impression was that males sustained more severe trauma than did females. Unlike adult females, older males were often extensively scarred or wounded on the head and shoulders. Males with tooth breakage often had two or more canine teeth broken off within 5 mm of the gum, exposing the pulp cavity. Few females had more than one broken canine tooth and none were found with such severe injury.

There are few data on how rapidly wounds can heal in wild mammals, however, I gathered some incidental observations of rates of healing. One adult male captured with an adult female in March had a large (> 30 cm^2) suppurating wound at the base of the left pinna and an 18 cm^2 open wound on the right foreleg. Eight months later, the wounds were completely healed and only minor scars were found. Another adult male captured in April had an open wound on his upper left thigh, approximately 50 cm long and six cm deep. The following spring, the resulting scar was not readily apparent through the fur even when specifically searched for.

4.4 Discussion

Considerable variation exists in the interbirth interval among and within populations of polar bears. Whereas three or more years between births is the norm in the more northern Canadian populations, two-year intervals are common in the western Hudson Bay population (Stirling and Latour 1978, Lentfer et al. 1980, Stirling et al. 1980, Ramsay and Stirling 1982). At present, I do not know why these differences exist.

If an adult female from the northern populations does breed in the spring when her cubs from a previous litter are two years old, separation from the cubs appears to occur early in the breeding season. By summer, almost all known-pregnant females were solitary. Yet, the proportion of females in each reproductive class, including females with 2-year-old cubs, was similar in both the spring and summer/autumn sampling periods (Table 4-1) suggesting that most females that were with two-year-old cubs when captured in spring probably did not breed in that year. Cubs might be abandoned by their mother or driven off, usually before but possibly after mating. Alternatively, a courting adult male may drive the cubs away from their mother. Anecdotal evidence suggests that all three forms of abandonment occur, just as in other species of bears (Herrero and Hamer 1977, Rogers 1977, Murie 1981). In most cases, however, a female would be expected to have control over when family break-up occurs because she would have a greater amount of reproductive investment at stake in a given litter than would an individual male (Trivers 1972).

Lactational anoestrus is common in mammals (Short 1984) and probably accounts for the low frequency of adult males with adult female polar bears still accompanied by cubs. Female bears of other species that lose cubs prematurely, either through death or abandonment, can breed again in the year of cub loss (Baker 1912, Erickson et al. 1964), if the loss occurs before or during the spring breeding season. Although seemingly infrequent in polar bears, breeding can occur in years when females are accompanied by newborn cubs in spring.

In certain theoretical life-history models, a female might prematurely abandon a current litter of cubs if the expectation were high of producing a greater number of cubs the next year (Tait 1980). Under such a model, single cubs would be most vulnerable to abandonment. Single cub-of-the-year litters, however, were not lost or abandoned more frequently than were cubs from larger litters. Yet, losses of two-cub litters were greater than would be expected if the death of each cub was an independent event. I do not know what the major causes of death are for young cubs. Some mortality factors (e.g. predation, starvation, unstable sea ice) might result in non-independent cub death and, hence, increased probability of loss of a whole litter rather than just one cub. Our data do not provide strong evidence in support of Tait's (1980) hypothesis of opportunistic cub abandonment, at least for polar bears.

Male and female polar bears have similar hunting methods and prey on the same species of seals (Stirling and Latour 1978). Similarity in diet is suggested by the like pattern of tooth wear observed in both sexes. The significantly greater degree of wounding, scarring, and tooth breakage in adult males (Table 4-3) is therefore probably not due to differing predatory interactions with seals but rather to overt aggression among males, primarily during the breeding season. Outside the breeding season, even prolonged intrasexual fighting among males does not result in injury (Latour 1981).

Females and males may interact aggressively over food resources or when a mother is defending her cubs; however, as females tend to avoid adult males, such events are probably infrequent (Stirling 1974). The low frequency of injuries seen on females suggests that intersexual aggression during courtship and intrasexual fighting are probably not common in this sex.

Periodontal disease and tooth breakage is frequent in some populations of black bears, especially among very old bears, but these injuries do not appear to be related to intraspecific strife (Rausch 1961, Rogers 1983). The extent of injuries sustained by adult male polar bears in all populations was striking to us, especially in spring during the breeding season when virtually all open wounds were noted. Similar patterns of injury and intense intrasexual fighting that might result in physical trauma have not been reported from other species of bears (Sparrowe 1968, Craighead et al. 1969, Herrero and Hamer 1977, Lindzey and Meslow 1977, Murie 1981), although Beecham (1980) and Young and Ruff (1982) anecdotally mention increased wounding in black bears during the breeding season. This suggests that there are differences between polar bears and other ursids in the degree of male intrasexual aggression displayed during the breeding season.

For all age classes of terrestrial bear species, males experience higher mortality rates than do females (Bunnell and Tait 1985). Much of current bear mortality may be hunter caused and hence not reflect historical conditions. Young and Ruff (1982), however, working with an unhunted black bear population demonstrated that adult males regulated population density, primarily by influencing subadult dispersal and mortality, especially of males. Through such mechanisms Bunnell and Tait (1981) proposed that adult males may increase their reproductive fitness by decreasing the density of male competitors within their home ranges. Female polar bears do not, however, maintain territories. Adult male polar bears may be unable to regulate male population density by selectively inducing subadult males to disperse because there is no natal territory for a subadult, of either sex, to disperse from. This probably results in similar sex-specific mortality rates, although their direct determination has not been made, with the consequence that tertiary sex ratios are approximately unity (Furnell and Schweinsburg 1984, Stirling et al. 1980, 1984).

The particular mating system adopted by a mammal is determined by a complex interplay of ecological and genetic factors. General ecological theory is not yet robust enough to provide unambiguous prediction of the mating systems to be expected for any species (Clutton-Brock and Harvey 1978). Nonetheless, generalized patterns can be determined for polar bears, *a posteriori*, that are consistent with some ecological models that have been proposed to account for differing mating systems.

Polar bears are highly sexually dimorphic, with males being about twice the size of females (Kingsley 1979). Since females breed at two to three year intervals or longer, fewer are available to breed in any year than are males. Functionally, therefore, the sex ratio of available breeders becomes skewed upward to at least two to three males per available female. If the largest males gain preferential access to oestrous females then the functional breeding sex ratio for the average male is skewed even further. Intrasexual competition among males for access to oestrous females and extreme sexual dimorphism would therefore be expected (Trivers 1972, Ralls 1977). Similar sexual asymmetry in the annual number of potential breeders is also found in other bear species (Bunnell and Tait 1981). The extent of local unpredictability in structure of arctic sea ice and associated availability of food, however, introduces an additional influence on polar bears that is not found in other ursids. In the eastern Beaufort Sea, potentially reproductive female polar bears (i.e. solitary adult females and adult females with two-year-old cubs) and adult males show a propensity to concentrate along active ice floe edges, whereas adult females with younger cubs tend to avoid such ice types (Table 4-2). The same patterns of distribution have been observed in other populations where the habitat is similar, such as eastern Lancaster Sound (population F) and in southeastern Baffin Island (population D) (Stirling et al. 1980, Schweinsburg et al. 1982). Even in areas where the ice types are more stable, such as in Franklin Strait (population E), regions of seal productivity or availability may vary among years and the bear distributions fluctuate accordingly (R.E. Schweinsburg, pers. comm.).

When food resources are predictable in space, then females of solitary species can distribute themselves accordingly while male distribution will be determined by the distribution of females. Male terrestrial bears can occupy fixed territories that encompass the permanent territories of several females (Bunnell and Tait 1981, Macdonald 1983). The seasonal and annual variation in the distribution of the ice types favoured by potentially breeding female polar bears, however, probably means that there is no advantage to individual males to maintain long-term exclusive dominance over locales fixed in space because there is low probability that they will overlap the ranges of oestrus females.

It is tempting to interpret the similar relative densities of adult male and solitary female polar bears (i.e. those likely to be in oestrus) in spring (Table 4-2) as a reflection of the males spacing themselves relative to that of solitary females. For males, already at a demographic disadvantage relative to the number of potential mates, the best strategy to adopt may be to space themselves out in each ice habitat type at the same density as that of solitary females. This would allow each male to make the best of a bad situation by ensuring that potential competitors for mates were at the lowest possible relative density.

To further minimize competition for mates, adult male polar bears may attempt to sequester oestrus females in regions where there would be little likelihood of encountering other males. Males may also remain with individual females for many days during which copulation may repeatedly occur. Multiple copulations may be necessary to induce ovulation in the female, a common feature of carnivore reproduction, and to ensure paternity by avoiding sperm competition (Milligan 1982). A similar pattern of breeding behaviour has been described for some brown bear populations (Herrero and Hamer 1977, Murie 1981). However, in those brown bear populations that congregate at high densities at human refuse tips, a situation somewhat analogous to that of polar bears concentrating along productive ice crack and lead systems, a different pattern of breeding behaviour has been reported. Under such artificial high-density situations, both male and female brown bears were promiscuous and the incidence of intrasexual aggression was low (Sparrowe 1968, Craighead et al. 1969).

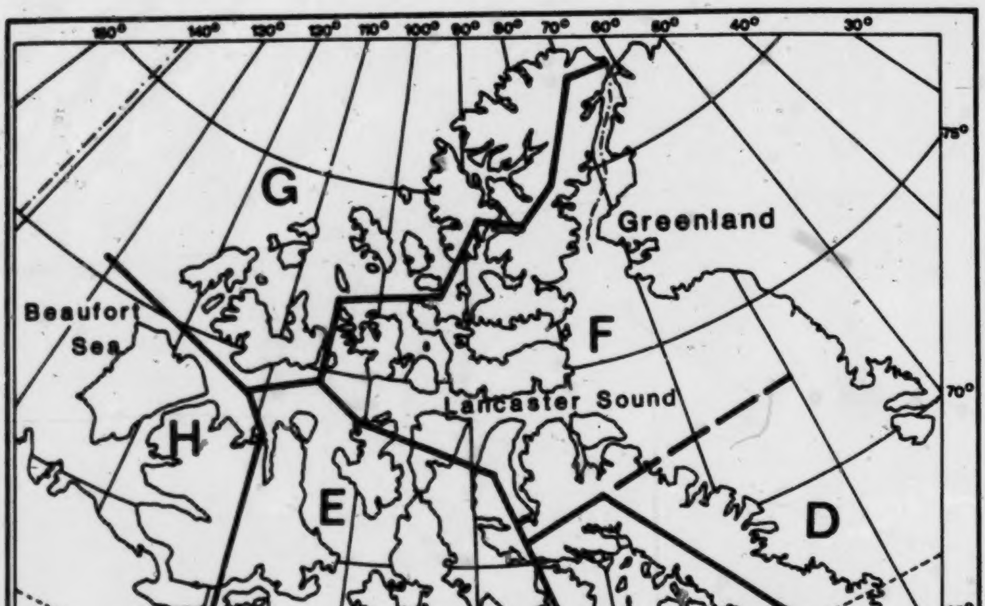
One consequence of the maintenance of stable territories is facilitation in recognition of neighbouring territory holders (Leyhausen 1965). Recognition of rival conspecifics allows an animal to adjust its agonistic behaviours in order to realize the maximum likelihood of success (van Rhijn and Vodegel 1980). Prior knowledge of individual opponents leads to adjustments in the nature of conflicts and a net reduction in time and energy expended to achieve resolution (Colgan 1983). The apparently labile social grouping of polar bears during the breeding season appears to result in a scramble competition among males for breeding opportunities and a higher incidence of direct intrasexual male aggression, and associated injuries, compared to other bears.

Latour (1981) proposed that the social play observed during summer and autumn in adult male polar bears inhabiting western Hudson Bay may allow the bears to assess the fighting capabilities of potential rivals at a time when resources are not at stake and facilitate the development of motor skills needed to compete successfully in agonistic encounters. Social play may thus offer the opportunity for the establishment of a loose hierarchical structure among participating adult males. This might result in a reduction in the severity or frequency of fights during male intrasexual conflicts. Certainly, young males could profit by determining their relative fighting capabilities and the probability of success against opponents of differing sizes prior to participating in full scale altercations (Leyhausen 1965). During the breeding season older males were more frequently found consorting with adult females than were younger males, suggesting that learning or experience in intrasexual competition may play a part in successful breeding. It may be noteworthy that adult social play has not been reported for species of bears that maintain stable territories (Henry and Herrero 1974).

The inability of male polar bears to defend regions that overlap territories of specific females might have further ramifications. The continual movements of females would probably not allow males to become familiar with local females with whom they may have mated. An individual male would therefore have a very low probability of being the father of the cubs in any family he might encounter. As a consequence, he might be expected to have little inhibition from killing cubs, if it could be done at little cost. Taylor et al. (1985) suggested that infanticide might be a strategy adopted by male polar bears to allow them breeding opportunities with the mothers of killed cubs, as has been suggested for other species (reviewed by Hrdy 1979, Hayssen 1984). This would appear not to be the explanation in all cases, however. To be a successful reproductive strategy for a male, infanticide would have to occur immediately before or during the breeding season. Yet many of the male infanticide cases cited by Taylor et al. (1985) were well outside the spring breeding season. I know of no data suggesting that infanticide is more common in polar bears during the breeding season than at other times. Infanticide by adult males, and associated early repeat breeding by females, would be expected to be most common in social species when a resident infanticidal male can supply access for a female to resources that compensates for her loss of current reproductive effort (Hayssen 1984) or in social and territorial species where males maintain temporary access to groups of adult females (Packer and Pusey 1983). Females of a relatively solitary and non-territorial species would, however, be expected to vigourously avoid infanticide. Normally, female polar bears with young cubs either actively avoid adult males or confront them aggressively (Table 4-3, Stirling 1974, Stirling et al. 1981). A male attempting to kill a litter of cubs in order to procure a breeding opportunity would, therefore, have to deal with a maternal defense. Such a reproductive strategy could result in injury to either the male or the female (Packer and Pusey 1983), either of which could jeopardize his fitness. In two recently reported incidents, both in the summer, adult males were found feeding on dead adult females while their orphaned yearlings watched from a distance (Lunn and Stenhouse 1985, S. Smith, pers. comm.). It seems likely that both of these females died while protecting their cubs. Assuming that a male could successfully kill a litter of cubs without incurring serious injury to himself or the female, in order to sire the next litter he would have to constrain or accompany the female until her oestrus in the next breeding season. I know of no evidence that suggests this occurs. Since females can outdistance males (Stirling 1974), achieving successful copulation, even during the breeding season, with an uncooperative female might prove difficult.

Further studies on polar bear mating behaviour and ecology would afford an opportunity to better determine how patterns of resource distribution influence the life-history options available to a solitary carnivore. The relatively simple ecosystem of the Arctic, the simple predator-prey food web of polar bears (one predator, two principle prey), and the open nature of the habitat make this a system particularly well suited to carry out and interpret such studies.

Figure 4-1. Map of northern Canada showing the approximate boundaries of discrete polar bear populations determined by mark - recapture data.


150°
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65°
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60°
65°
70°
110°
100°
90°
80°
G
Greenland
Beaufort Sea
F
Lancaster Sound
H
E
D
C
Baffin Island
Northwest Territories
Hudson Bay
A1
A2
A3
Manitoba

Table 4-1. Adult polar bears captured in the northern Canadian Arctic, ordered by season of capture and accompanying bears, (1970 - 1985).

Reproductive class	MAR - MAY		JUN - NOV	
	n	% of total	*n*	% of total
Adult female with cubs-of-the-year	174	27	35	27
Adult female with cubs-of-the-year and accompanying adult male	1	0.2	1	1
(proportion with adult males)	(0.01)		(0.03)	
Adult female with yrlg	117	18	27	21
Adult female with yrlg and accompanying adult male	2	0.3	0	0
(proportion with adult males)	(0.02)		(0.00)	
Adult female with 2-yr-olds	74	11	15	11
Adult female with 2-yr-olds and accompanying adult male	3	0.5	1	1
(proportion with adult males)	(0.04)		(0.06)	
Lone adult female	190	29	50	38
Lone adult female and accompanying adult male	91	14	2	2
(proportion with adult males)	(0.32)		(0.04)	

Total females	652	100	131	100
Solitary adult male	557	87	86	96
Adult male and accompanying adult female	80	13	4	4
Total males	637	100	90	100

Table 4-2. Proportion of bears seen on different ice types relative to the proportion of distance searched on each ice type; an index of relative abundance. A total of 441 bears were seen during 65,658 km of search routes flown. Bears ordered by sex and reproductive status. Data compiled from Stirling et al. (1981) in the eastern Beaufort Sea (1971-1977). Ice types described in text.

Reproductive class	Ice type and distance searched		
	Type 1 23,693 km	Type 3 13,664 km	Type 4 28,301 km
Adult females with cubs-of-the-year or yearling cubs (*n* = 77)	.44/.36 = 1.22	.14/.21 = 0.69	.41/.43 = 0.97
Adult females with two-year cubs (*n* = 22)	.09/.36 = 0.25	.64/.21 = 3.06	.27/.43 = 0.63
Adult females without cubs (*n* = 85)	.11/.36 =0.29	.44/.21 = 2.09	.46/.43 = 1.06
Adult males (*n* = 257)	.08/.36 = 0.22	.45/.21 = 2.15	.48/.43 = 1.10
Total (*n* = 441)	.15/.36 = 0.42	.40/.21 = 1.93	.45/.43 = 1.05

Table 4-3. Age-specific tooth wear, tooth breakage, wounding, and scarring prevalence for female and male adult polar bears handled in the Canadian Arctic (1983 - 1985).

Age	Females					Males				
	n	Index of mean incisor wear	No. with canine breakage	No. with wounds	No. with scars	*n*	Index of mean incisor wear	No. with canine breakage	No. with wounds	No. with scars
05	21	1.0	1	-	1	17	1.0	-	1	1
06	11	1.0	-	-	-	12	1.0	-	1	3
07	12	1.0	-	-	-	9	1.0	-	1	-
08	14	1.1	-	1	-	13	1.2	-	1	4
09	5	1.4	1	-	-	12	1.7	-	3	7
10	10	1.3	-	1	1	7	1.3	1	-	3
11	8	1.5	-	-	2	9	1.8	3	1	5
12	10	1.8	1	-	-	7	1.6	1	-	4
13	10	1.9	2	-	1	7	2.0	1	5	7
14	13	1.8	1	-	2	6	1.8	4	3	6
15	9	1.9	-	-	-	6	1.7	2	1	5
16	12	2.0	1	1	1	8	2.0	3	3	6
17	7	1.6	-	1	3	5	2.0	-	-	5
18	13	1.9	-	1	-	6	2.3	5	3	6
19	9	2.0	-	-	2	7	2.0	6	1	7
≥20	22	2.6	4	-	2	12	2.8	8	2	12
Total	186		11	5	15	143		34	26	81
Proportion of total			(0.06)	(0.03)	(0.08)			(0.24)	(0.18)	(0.57)

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5. SEASONAL CHANGES IN SERUM UREA AND SERUM CREATININE OF POLAR BEARS FROM WESTERN HUDSON BAY

5.1 Introduction

Most Holarctic bears of the ge[illegible] *Ursus* enter a den each winter for a prolonged period of dormancy without access to food or water and without lowering body temperature (Lindzey and Meslow 1976, Nelson et al. 1973). The time spent in winter dens varies with species and location, generally being longer for more northerly populations (Johnson and Pelton 1980). During this time, all energetic and maintenance requirements are met from body stores, primarily adipose tissue. Lean body mass remains relatively constant, and net urea production is negligible (Nelson et al. 1975, Ahlquist et al. 1984). Cubs are born while females are still in their dens and are nursed for several weeks before emergence (Matson 1954).

A period of hyperphagia and extensive deposition of adipose tissue precedes den entry for black bears (*U. americanus*) and brown bears (*U. arctos*) (Nelson 1980, Kingsley et al. 1983). Immediately before denning, however, black and brown bears characteristically move away from their summer centres of activity and reduce food intake or cease feeding entirely (Craighead and Craighead 1972, Tietze and Ruff 1980). After spring emergence, feeding does not usually begin immediately (Nelson 1978).

During winter dormancy and during anorexia immediately before and after denning, the serum concentration of urea declines while that of creatinine rises relative to concentrations in bears actively feeding in summer. Consequently, the ratio of urea to creatinine (U/C) is characteristically lower during denning and associated non-feeding periods in bears than at other times of the year (Nelson et al. 1984). Creatinine is formed endogenously from creatine as a result of normal muscle catabolism. Serum levels are maintained primarily as a function of kidney glomular filtration rate and are little affected by diet. Serum urea, by contrast, is affected both by diet and by renal function (Britton 1974). Black bears that fail to enter winter dormancy or bears starved during summer do not reach the low U/C ratios characteristic of dormant bears and may become uremic (Nelson et al. 1975, Nelson 1978). As a consequence, Nelson et al. (1984) proposed that a U/C ratio of 10 or less in bears is an indicator of biochemical and physiological adaptations for long-term fasting at near-normal body temperature.

Polar bears (*U. maritimus*) differ from other bears in that only pregnant females regularly enter dens in autumn (Harington 1968). Males and non-pregnant females remain active on the arctic pack ice throughout all but the most inclement winter weather, feeding primarily on ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977). Unlike the high quality plant foods that most black and brown bears depend on, seals are available for capture throughout winter. For adult polar bears the blubber of a seal is preferred food, the remainder of the carcass frequently being abandoned (Stirling 1974, Stirling and McEwan 1975, Smith 1980). In contrast, juveniles, subadults, and lactating adult females may consume most or all of a killed seal and scavenge fat-free carcasses abandoned by other bears (Stirling and McEwan 1975).

The propensity of some adult polar bears to choose fat when both fat and muscle tissue are available suggests that they are able to meet their metabolic requirements primarily from dietary fat. If true, then bears adopting such behaviour may be in a physiological state similar to that of a hibernating bear. Body protein would be spared by a reduction in urea production and by recycling nitrogen wastes from protein catabolic pathways into protein synthetic pathways. Thus, polar bears could survive long periods without an exogenous protein source and without significantly reducing their lean body mass. They could rapidly replenish their fat stores (Best 1984) when seals were abundant.

The sea ice melts completely each summer in Hudson Bay and polar bears there are forced ashore until ice reforms in the autumn. This is in marked contrast to the situation in most of the rest of polar bear range in Canada where sea ice, and hence access to seals, remains year round. Along western Hudson Bay in northeastern Manitoba, the period ashore is from late July - early August to late November - early December for all but pregnant females. Pregnant bears do not return to the sea ice until the following spring (Stirling et al. 1977a). In the High Arctic, polar bears feed heavily on recently-weaned ringed seals in late spring and early summer (Smith 1980, Stirling and McEwan 1975) and the bears of Hudson Bay probably do the same. They are, therefore, probably near their maximum annual weight when they come ashore in August. While ashore, however, most polar bears appear to feed little or not at all and lose weight, except for a small number that feed at the Churchill refuse dump (Russell 1975, Knudsen 1978, Latour 1981, Lunn and Stirling 1985). Many of the bears using the dump gain rather than lose weight (Lunn and Stirling 1985). The summer and autumn feeding patterns of polar bears in western Hudson Bay, even those of pregnant females, are in marked contrast to those of black and brown bears which forage actively and gain considerable weight before entering dens for the winter (Tietje and Ruff 1980, Kingsley et al. 1983).

Results of analyses of serum for 13 free-ranging polar bears captured in 1978 during the on land period in northwestern Manitoba showed U/C ratios lower than ten (Nelson et al. 1983). Coupled with the observation that most polar bears do not actively feed while ashore, these data suggest that they may have been in a physiological state similar to that of a winter-dormant black bear.

In this study, I document the serum levels of urea and creatinine of polar bears during their time on land. As polar bears have different seasonal opportunities for feeding than do terrestrial bears, comparison of blood parameters at times of feeding and not-feeding may offer insight into some of the metabolic adaptations of polar bears.

5.2 Methods

During studies on the ecology of polar bears in western Hudson Bay, free-ranging animals were captured in three different seasons: (1) in spring (March), as adult females and their new-born cubs-of-the-year emerged from their winter dens after almost eight months ashore; (2) in summer (July and August), when all age and sex classes first came ashore from the melting sea ice; and (3) in autumn (October and November), after all age and sex classes had been ashore for two to three months. The latter sample was divided into two groups. Bears captured in autumn at or near the Churchill refuse dump, where bears had the opportunity for feeding, were considered separately from those not at the dump.

Polar bears were captured in the Hudson Bay lowlands of Manitoba in the region bounded by the mouth of the Churchill River (58°50' N, 94°15' W) and the Nelson River (57°30' N, 92°30' W). The region is characterized by long cold winters and short cool summers (Thompson 1968). Major plant communities are sub-arctic tundra near the coast and tundra-spruce (*Picea* spp.) forest ecotone further inland.

Because of logistic limitations, no bears were sampled when they were hunting seals on the ice of Hudson Bay during winter and spring. For comparative purposes, however, five blood samples were obtained in April from polar bears on the sea ice of the central Canadian High Arctic near Resolute, NWT (approximately 75° N, 95° W). These samples were obtained at a time when the bears had access to seals but before the period of the greatest weight gain in late spring.

Bears were captured by chemical immobilization using either a 1:1 mixture of ketamine hydrochloride and xylazine hydrochloride at 200 mg/ml each or a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride at 300 mg/ml each (Lee et al. 1981, Haigh et al. 1985). All drugs were administered using standard dart equipment shot from a helicopter (Lentfer 1968, Larsen 1971).

Blood samples were drawn from the femoral vein into 50 ml sterile syringes and then transferred to sterile containers. Samples were kept cool (3° C) until clotting had occurred then centrifuged until the serum separated from the cells. Serum was stored at -20° C until analysis. Serum urea nitrogen and serum creatinine were determined using the methods of Nelson et al. (1984).

A total of 357 blood samples were collected in northeastern Manitoba: 52 in March, 1983 and 1984; 138 in July - August, 1983 and 1984; 145 in October - November, 1982 and 1983; and 21 from bears at the refuse dump in October - November, 1982 and 1983.

Three bears displayed atypical behaviour at capture and their blood data were omitted from the general analysis. These were a 16-year-old female with two accompanying cubs-of-the-year handled in October 1983 when they were feeding on a caribou (*Rangifer tarandus*) carcass for at least three days prior to capture; a five year old solitary female feeding on a seal when handled in August, 1984; and a seven-year-old female captured at her winter den in March, 1984 with a single dead cub-of-the-year. Except for bears foraging at the refuse dump, the two summer/autumn captured bears were the only ones on shore that were known to have fed immediately before capture.

In order to approximate a normal distribution of variables with equal variances, blood data were transformed to their natural logarithm (Sokal and Rohlf 1981). Only females were sampled in spring while, in other seasons, both sexes were sampled. Differences in mean blood parameters between seasons were compared by analysis of variance and pairwise multiple t-tests. Bonferroni levels of significance were used to test for differences between sample means (Games 1971). Differences in U/C ratios between probable pregnant and non-pregnant bears during summer and autumn, and between adult females with accompanying cubs-of-the-year and solitary adult females in spring were determined using two-tailed Mann-Whitney U-tests. All statistical calculations were carried out using BMDP (1981) Statistical Software (Department of Biomathematics, University of California, Los Angeles).

5.3 Results

No significant differences were found in the mean U/C levels between sexes in summer (female $\bar{X}$ = 13.4, n = 61; male $\bar{X}$ = 12.8, n = 77; F = 0.203, df = 1, P = 0.65), in autumn (female $\bar{X}$ = 6.7, n = 62; male $\bar{X}$ = 7.6, n = 83; F = 1.61, df = 1, P = 0.21), and at the dump (female $\bar{X}$ = 14.8, n = 10; male $\bar{X}$ = 23.3, n = 11; F = 3.39, df = 1, P = 0.08). Consequently blood parameter data for both sexes were pooled for subsequent analyses.

There were significant between-season differences in the mean U/C level for bears for serum urea (F = 19.7 ; df = 3; $P = \ll 0.001$), serum creatinine (F = 25.5; df = 3; $P = \ll 0.001$), and U/C (F = 37.7; df = 3; $P \ll 0.001$). The mean U/C ratio was lowest for bears emerging from dens in spring and highest for bears handled at the dump (Table 5-1). There was no significant difference between mean U/C ratios of bears handled in summer and those handled at the dump (t = 1.47, Bonferroni P = 0.14). Bears handled in spring and autumn also had mean U/C ratios that were not significantly different (t = 0.36, Bonferroni P = 0.72). All other pairs of mean U/C ratios, however, were significantly different (Bonferroni $P \ll 0.001$).

Similar comparative relationships held for serum urea levels (Table 5-1). There was no significant difference between mean serum urea levels from bears captured in summer and those at the dump (t = 0.03, Bonferroni P = 0.98). Bears captured in spring and autumn had mean serum urea levels that were also not significantly different (t = 1.12, Bonferroni P = 0.26). All other comparisons of mean serum urea levels were significantly different (Bonferroni $P < 0.001$). The mean difference in serum creatinine was not significantly different between bears captured in spring and autumn (t = 1.63, Bonferroni P = 0.10) but was significantly different for all other comparisons (Bonferroni $P < 0.001$).

Females captured in spring had been fasting for 4 - 8 months and most were accompanied by recently born cubs-of-the-year. Six bears captured in spring, however, were without cubs. Although these solitary females had presumably been dormant, their over winter energy demands were probably lower than if they had been lactating at the time of capture. There was no significant difference in the mean U/C ratio between the two groups ($U = 89.0$, $P = 0.17$). Twelve adult females in autumn were judged to be pregnant as they had elevated serum progesterone levels (Chapter 3). These bears had mean U/C ratios significantly lower than the other bears handled in autumn ($U = 345$, $P < 0.001$).

Individual U/C ratios for bears captured at the garbage dump were widely scattered (Fig. 5-1). The amount of time that a bear spent at the dump prior to capture usually was not known and probably varied between individuals. The two lowest U/C ratios among the bears sampled at the dump, however, were for bears known to be handled on their first day there, presumably before they had been able to eat very much.

The adult female that was feeding on a caribou in autumn had serum levels of 124.5 mg urea/dl, 1.4 mg creatinine/dl, and a U/C ratio of 88.9. The female feeding on a seal had serum levels of 73.3 mg urea/dl, 1.5 mg creatinine/dl, and a U/C ratio of 48.9. The female captured in spring with a dead cub-of-the-year had serum levels of 293.8 mg urea/dl, 12.2 mg creatinine/dl, and a U/C ratio of 24.1. The values of serum urea and the U/C ratio for the females that were feeding when captured were higher than those recorded for any other bear sampled, including bears captured at the refuse dump. Conversely, their serum creatinine levels fell within the range of the other bears. In contrast, the female with the dead cub had the highest recorded levels of both serum urea and creatinine. There were fresh urine stains in the snow around her den at capture and, one month later, when she was resighted at the same location. Urine stains were not observed in the snow near any other adult female handled in spring ($n = 128$). Her carcass was found near the den site in August, 1984 and she probably died without returning to the sea ice.

Table 5-2 shows comparative blood parameters for the five bears handled on the sea ice in spring. The two females and the youngest male had U/C ratios as high or higher ($\bar{X}$ = 56.4) than any bear summarized in Table 5-1. The two males, however, had U/C ratios less than 1/3 that of the other three. Nothing is known of the recent feeding regimen of any of these bears although it is probable that all had access to seals.

5.4 Discussion

My findings confirm and extend those of Nelson et al. (1983) who noted similar low U/C ratio levels in a small number of polar bears on land during autumn. Mean U/C ratios declined during the period on shore and, by autumn, approached the mean level for female bears emerging from dens in spring after an overwinter fast. Bears with the highest mean U/C levels were those that had recent access to food. Bears captured soon after coming ashore in summer may have been able to feed on seals just prior to their time of capture (Jonkel 1970) and might, therefore, be expected to still show relatively elevated U/C levels. Bears in autumn that had opportunity to feed on garbage had significantly higher U/C ratios than did bears not feeding on garbage. Similarly, the adult females known to have been feeding on seal or caribou had the highest U/C ratio recorded of any bears handled in their respective seasonal samples.

Unfortunately, no comparable data are available for bears on the sea ice of Hudson Bay where seals are accessible. The small sample obtained from the central High Canadian Arctic in April are bears that could have recently fed on seals. The U/C ratios for three of these bears were higher than for the bears handled on shore in western Hudson Bay, with the exception of the females known to have been feeding, suggesting that all three had recently fed. The two 10-year old males with considerably lower U/C ratios may have fasted prior to capture or consumed only the blubber layer of seals. If active polar bears can recycle urea from catabolized protein, then a diet high in fat and low in protein may result in a low serum U/C ratio, similar to that of a hibernating bear, for long periods of time. Although conclusions based on a sample of five are unwarranted the data are consistent with the age- and sex-specific feeding behaviour of free-ranging bears on the sea ice (Stirling 1984, Stirling and McEwan 1975, Smith 1980).

The female polar bear that voided urine in spring at her den site displayed symptoms similar to those of a black bear that failed to achieve winter dormancy while in captivity (Lundberg et al. 1976). In both bears, serum urea concentrations were considerably higher than those of dormant conspecifics, both voided urine, and both had lost a higher proportion of body weight than did successfully dormant animals. The high serum urea levels and extreme serum creatinine concentration of this polar bear, more than six times the mean value for other females handled in spring, is characteristic of an uremic animal (Doolan et al. 1962). These data suggest that some female bears cannot achieve or cannot maintain the physiological state necessary for successful dormancy over winter.

While ashore, most polar bears fast, yet when high quality food becomes available, such as at a refuse dump, they are capable of using it. Although infrequent along western Hudson Bay, carrion, including carcasses of bears that have died, are fed on opportunistically by polar bears of all age and sex classes (Jonkel 1970). Polar bears are also known to eat sedges (*Carex* spp.) and berries (eg. cranberries - *Vaccinium* spp., crowberries - *Empetrum nigrum*) while on land (Russell 1975, unpublished data). There are no quantitative data to determine the extent to which polar bears feed on plant foods during their tenure on land, but several lines of circumstantial evidence suggest that feeding rates are low. The time spent foraging by polar bears in summer and autumn is considerably less than that spent by black and brown bears (Pearson 1975, Knudsen 1978, Garshelis and Pelton 1980, Latour 1981, Lunn and Stirling 1985). Whereas black and brown bears feed intensively on berries and mast in late summer through early autumn and acquire considerable fat stores, most polar bears in western Hudson Bay, including pregnant females, lose weight during summer and autumn (Chapter 3). The varied and largely herbivorous diet of black bears in summer results in their U/C ratios being elevated (Nelson et al. 1984). Polar bears show falling U/C ratios during the period on land. Although the effects of different dietary regimens on serum U/C ratios in bears is not known, I assume that foods available to polar bears while on land would affect serum U/C levels in black and polar bears similarly.

Further evidence for low rates of herbivory is offered by the rarity of polar bear faeces, even in areas with high polar bear densities throughout the on land period such as along beaches and at points of land on the coast. If polar bears were eating large quantities of plant matter during their time on land then, as mammals with simple non-ruminant stomachs (Bunnell and Hamilton 1983), they should produce large quantities of faecal matter (Roth 1980). We have never found high densities of polar bear scats in six years of incidental search during our research program. Russell (1971, 1975) surveyed approximately 50 km^2 of coastal habitat known to have high densities of polar bears through the summer and autumn. As many as 329 individual bears were known to spend part or all of the on land period in his search areas. Yet he only collected 445 scats, some likely one or more years old, over a two year period.

Fasting for extended periods may result in epithelial changes in the gut that must be reversed before nutrient uptake can occur after renewed feeding. Low levels of intake of plant matter, such as displayed by polar bears when ashore in northeastern Manitoba, may be a means of slowing or halting gut epithelial changes during periods when seals are unavailable. Adult female polar bears, emerging from overwinter dens in spring, regularly eat small quantities of plant matter (Hansson and Thomassen 1983, Ramsay and Andriashek 1986).

Relative to their feeding regimen, the pattern of serum urea, serum creatinine, and their ratio for polar bears was similar to that determined for black bears (Nelson et al. 1984). In both species serum urea levels were highest at times when feeding and lowest at times when fasting, while serum creatinine levels showed a reverse pattern. Unlike black and brown bears, however, most polar bears in autumn were not about to enter overwinter dens. Except for pregnant females, the majority of polar bears in autumn return to the sea ice and remain active all winter. Their low U/C ratios at that season suggest that, although active and not in dens, they were in a physiological state similar to that of a dormant bear. Bears that did have access to food in autumn, such as at a garbage dump or a carcass, did eat and showed expected elevated U/C ratios. Thus, polar bears appear able to switch facultatively between physiological states in response to the availability of suitable food items and without regard to the season. This is in contrast to black bears that can only adapt to extended fasting in certain seasons but not others (Nelson et al. 1975, Nelson 1978).

Arctic marine habitats vary in productivity, both seasonally and annually (Nemoto and Harrison 1981). Seal distribution, abundance, and availability to bears can vary markedly both within and between years (Stirling et al. 1977b). The ability of polar bears to be able to adopt a physiological state conducive to long-term fasting during times of food shortage and yet be able to rapidly exploit food when available appears to be well suited to existence in an environment in which availability of suitable prey may vary in an unpredictable way.

Figure 5-1. Mean seasonal level (standard error) of serum U/C ratio for polar bears captured in northeastern Manitoba, October 1982 - March 1984, by season of capture. (●) indicate values for individual animals.

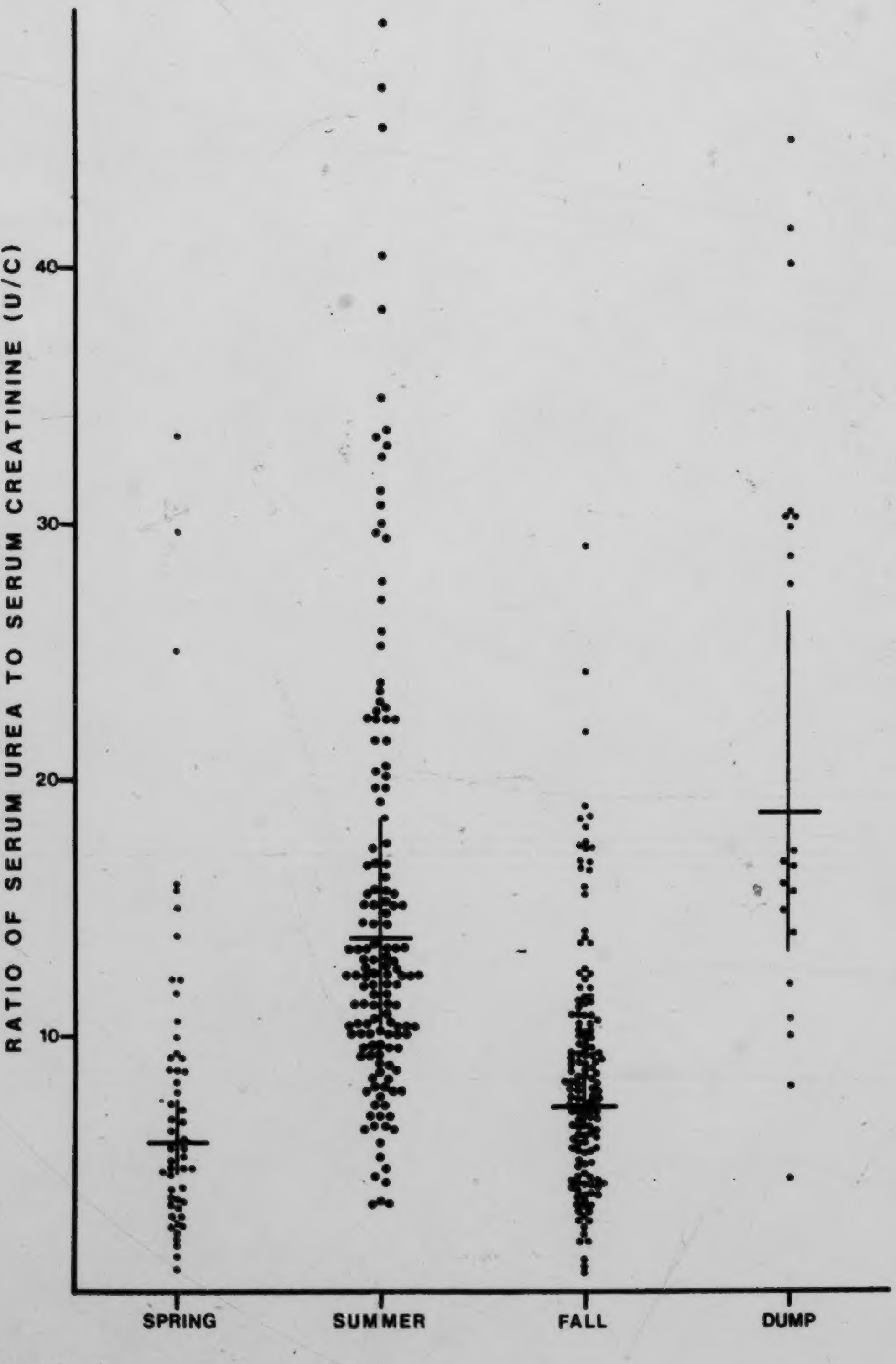
RATIO OF SERUM UREA TO SERUM CREATININE (U/C)
40
30
20
10
SPRING
SUMMER
FALL
DUMP

Table 5-1. Values of serum levels of urea (mg/dl), creatinine (mg/dl), and U/C ratio for free-ranging polar bears handled on land in northeastern Manitoba during four sampling periods (1982 - 1984). Statistics were determined from data transformed to their natural logarithm.

	Spring (n = 53)	Summer (n = 138)	Autumn (n = 145)	Dump (n = 21)
UREA (mg/dl) mean (± S.E.)	10.7 (8.4, 13.6)	20.0 (17.9, 22.3)	13.3 (11.7, 15.1)	21.9 (16.0, 30.0)
range	1.3 - 57.5	3.7 - 55.4	1.1 - 46.3	6.2 - 45.3
median	10.8	20.6	15.4	22.0
CREATININE (mg/dl) mean (± S.E.)	1.9 (1.7, 2.1)	1.5 (1.4, 1.7)	1.9 (1.7, 2.0)	1.2 (0.9, 1.5)
range	0.9 - 2.7	0.6 - 3.0	0.8 - 2.8	0.6 - 2.6
median	1.9	1.6	1.9	1.2
U/C mean	5.7 (4.5, 7.3)	13.1 (11.5, 14.8)	7.2 (6.3, 8.2)	18.8 (13.4, 26.4)
range	0.7 - 33.3	3.5 - 47.0	0.7 - 29.0	4.4 - 45.1
median	5.5	12.5	7.9	16.7

Table 5-2. Serum urea and serum creatinine levels for polar bears handled on the sea ice of the central Canadian Arctic, April, 1984.

Sex	Reproductive status	Age (years)	Serum urea (mg/dl)	Serum creatinine (mg/dl)	U/C ratio
F	alone	04	88.4	1.2	73.0
F	with 2 cubs-of-the-year	10	63.9	1.4	46.3
M	alone	06	47.0	0.9	50.0
M	alone	10	17.9	1.0	17.7
M	alone	10	13.7	1.8	7.6

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6. PHYSIOLOGICAL CONSTRAINTS ON LIFE-HISTORY PHENOMENA: THE EXAMPLE OF SMALL BEAR CUBS AT BIRTH[1]

6.1 Introduction

Attempts to explain ecological phenomena generally rely on simple optimality criteria involving limited sets of variables. Bounds on the adaptive responses available to meet particular ecological challenges are often not considered, and discrepancies between empirical observations and model predictions are frequently attributed to lack of model resolution (Pyke 1984). It is becoming clear, however, that the processes of adaptation are closely linked to important physiological constraints on the ability of organisms to achieve global ecological optima (Gould and Lewontin 1979). This study examines how such physiological constraints may have influenced an important life-history characteristic of the eutherian mammals, *viz*. weight at birth.

A log-linear relationship between litter weight and weight of parturient mother has been documented for the eutherian mammals (Leitch et al. 1959, McKeown et al. 1976). Bears (Ursidae), which give birth to relatively small litters of tiny, immature neonates, display the most extreme deviations from the regression of litter weight on maternal weight among the eutherians (Case 1978, Frazer and Huggett 1974, Leitch et al. 1959, McKeown et al. 1976, Pond 1977). Depending on the regression formula used, litter weights for bears are from 1/3 to 1/10 of that predicted for female mammals of comparable size (Leitch et al. 1959, McKeown et al. 1976). Such anomalous exceptions to generalized allometric relationships are, by definition, rare (Calder 1984), but they are of particular importance to general ecological theory because of the insight they may provide into constraints bounding life-history phenomena. In this paper I propose that the altricial ursid pattern of producing small neonates, and the consequent switch from trans-placental to mammary nourishment, is an adaptive response to physiological constraints associated with supporting foetal development while in a state of hibernation and without access to food.

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A brief overview of bear natural history is germane to the hypothesis. Because data on other species are sparse, this review focuses on the Holarctic bears: the American black bear (*Ursus americanus*), the brown bear (*U. arctos*), and the polar bear (*U. maritimus*). Bear litter sizes vary from one to four with a modal litter size of two for most populations (Craighead et al. 1969). Bears breed in the spring but implantation is obligately delayed until autumn (Wimsatt 1963). A pregnant female enters a winter maternity den close to the time of implantation, giving birth there approximately 50 days after implantation (Hensel et al. 1969, Wimsatt 1963). The length of time spent in winter dens varies with species and location, and it is generally longer for more northerly populations (Johnson and Pelton 1980). The winter den of a bear is thermally insulated, making the microclimate of an occupied polar bear den even in the High Arctic relatively benign (Blix and Lentfer 1979). Cubs are nursed huddled within their mother's fur until the family emerges in the spring, by which time the cubs have reached the weight for mammalian neonates predicted by regression (Leitch et al. 1959). Thus, for bears the maternity den performs a protective function partially analogous to that of the uterus.

During winter dormancy, a female bear neither eats nor drinks, maintaining herself entirely through the metabolism of fat stores (Nelson 1980). A bear in winter dormancy is not simply a starving bear. Rather it is in a physiological state similar to that of hibernation but without the marked reduction in body core temperature displayed by classical hibernating mammals (Folk et al. 1980, Lyman 1982). Body protein is protected, except when it is used to meet the growth and metabolic requirements of the developing foetuses and nursing neonates, and no urine is voided (Lundberg et al. 1976, Nelson 1980, Nelson et al. 1973). No other mammals, except some of the large

Mysticeti cetaceans, go without food and water for extensive periods during active gestation (Frazer and Huggett 1973); and only bears, some cetaceans, and some phocid pinnipeds fast through part or all of the lactation period (Fedak and Anderson 1982, Lockyer 1981).

6.2 Physiological considerations

Mammals exhibit a number of physiological responses to the problems of supplying sufficient metabolites to body tissues and coping with intermediary metabolic products and wastes while fasting. The primary metabolic response to the low blood glucose levels that accompany extended fasting is the release of triglycerides and free fatty acids (FFA) from adipose tissue as alternative substrates of oxidation. This in turn leads to an increase in the rate of ketone body formation in the liver (Krebs et al. 1971). Ketone bodies are required by the central nervous system, which can use only these or glucose, but not FFA, as oxidative substrates (Cahill and Aoki 1980). The use of FFA and ketone bodies during fasting, in lieu of glucose, serves to spare body protein that would otherwise be broken down by gluconeogenesis.

For pregnant females the problems associated with fasting are compounded since both nutrient supply and waste clearance for foetuses must be mediated by the mother across the placenta (Felig and Lynch 1970, Freinkel et al. 1972). Not surprisingly, the metabolic responses of gravid females to fasting are more rapid and markedly more extreme than those observed in non-gravid conspecifics (Freinkel et al. 1972, Girard et al. 1977). Although these responses are well documented for a number of mammalian species, the details of the metabolic interrelationships between mother and foetus during fasting are less well understood and have not been described for any of the Ursidae. In reviewing the data available for other mammalian species, I have assumed that the metabolic processes involved are not qualitatively different in bears (Battaglia and Meschia 1981).

In contrast to a pregnant female, which can readily catabolise FFA during fasting, dependence on fatty acids as an energy source by the mammalian foetus has not been observed (Girard et al. 1979, Hahn 1979, Roux and Yoshioka 1970, Warshaw 1979). Appreciable trans-placental transfer of FFA does occur in some species, especially during fasting when maternal plasma FFA levels are elevated, but these appear to be deposited in foetal adipose tissue or used for structural requirements (Edson et al. 1975, Elphick et al. 1975, Girard et al. 1977). Although some increase in enzymatic activity for FFA oxidation occurs in foetal tissue during maternal fasting, the increases are significantly lower than those that occur post-partum (Kimura and Warshaw 1983). *In vitro* analyses also indicate that foetal tissues have little or no ability to use FFA for meeting energy requirements (Freund et al. 1984, Roux and Myers 1974).

The reason for the lack of FFA catabolism in the mammalian foetus is puzzling (Hochachka and Somero 1984), especially considering that the neonate can catabolize fatty acids as the primary source of energy within a few hours of birth (Hahn 1979). Although the details of the transfer process are not fully understood, it is clear that FFA do not cross the placenta as readily as glucose or ketone bodies (Dancis et al. 1976, Robinson and Williamson 1980), possibly limiting their availability as a foetal substrate. Glucose and FFA also differ in relative oxygen requirements during catabolism, with FFA requiring more oxygen per molecule of ATP produced than does glucose (Hahn 1978). Although fetal metabolism is fully aerobic under most conditions (Harned 1978), it is nonetheless very high and relatively constant per kilogram of foetal weight (Battaglia and Meschia 1978, 1981), in marked contrast to post-natal mammals in which oxygen consumption is allometrically related to body mass. Additionally, foetuses exist in a state of relatively low oxygen availability because of the lack of direct atmospheric exchange with their circulatory system. The total oxygen stores of a near-term foetus are probably less than 1 - 2 minutes (Longo and Power 1976), and a reduction in maternal oxygen supply rapidly leads to foetal hypoxia and associated uterine growth retardation

(Van Geijn et al. 1981). Furthermore, unlike glucose, the catabolism of FFA is strictly aerobic in all eukaryotes (Lehninger 1975). Therefore, a foetus may be constrained from large scale dependence on FFA as an energy source because this would increase both the potential for limitation of its growth rate and its vulnerability to energy shortages and tissue damage during periods of oxygen stress. These problems may be of particular relevance for a foetus developing within a hibernating bear because oxygen concentrations in the den are reduced due by the limited exchange of gas with the external atmosphere (Withers 1978).

Although maternal fat stores may not be directly available to supply the energy requirements of the developing foetus they could, in theory, be converted to ketone bodies for subsequent use as the principle oxidative substrate (Cahill 1972). However, the extent to which foetuses metabolize ketone bodies as an energy source, in lieu of glucose, during long-term maternal starvation has not been determined. The sustained maternal levels of circulating ketone bodies that would be required to produce substantially larger foetuses than those typical of bears might lead to ketonaemia, consequently interfering with the physiological adaptations required for survival under conditions of no available food or water (reviewed by Nelson 1980).

The alternative to the direct or indirect use of maternal fat stores to supply foetal energy demands is a reliance on maternal amino acids for gluconeogenesis throughout gestation. However, this might deplete maternal body protein so as to jeopardize survival. Thus, it seems clear that a considerable selective advantage would accrue to any adaptation making maternal fat stores available to developing young. Although there appear to be constraints on this adaptation *in utero*, these stores can be directly incorporated into milk, the sole source of neonatal nourishment. In contrast to foetuses, early neonates have a rapidly rising capacity for oxidising FFA and may meet most or all of their energy requirements from fatty acid oxidation (Hahn 1979), while limiting gluconeogenesis, a major pathway for energy acquisition in the foetus (Miller

1969, Snell 1982, Snyderman 1978). Bear milk is higher in total solids, fat, and protein, and lower in carbohydrates, than that of other carnivores and of most other terrestrial mammals; it more closely resembles that of pinnipeds and cetaceans (Jenness 1974, Jenness et al. 1972). More than 50% of these total solids consist of fatty acid chains of 16 carbon atoms or more, probably mobilized directly from adipose tissue (Jenness et al. 1972). By nursing small neonates instead of maintaining developing foetuses, a fasting female could thus use her fat stores and avoid the loss of body protein resulting from gluconeogenesis, simultaneously eliminating the potential problem of pH imbalance from ketoacidosis that could accompany high rates of foetal ketone body utilization. Furthermore, the potential problem of extreme ketonaemia would not be simply passed onto her neonate. Even a neonate depending entirely on FFA as an energy source would only be constrained to use ketone bodies only in its central nervous system. Other tissues could catabolize FFA, and high levels of circulating ketone bodies are common in all mammalian neonates because of the ketogenic nature of their diets (Warshaw 1979).

There appear to be no fundamental physiological or developmental constraints to the production of extremely small neonates that undergo considerable development while nursing. All metatherian mammals at birth are very tiny relative to their mother and are in an extremely immature state (Tyndale-Biscoe 1973), but they begin suckling almost immediately and continue their development, until independence, solely on a diet of maternal milk. The duration of lactation in metatherians is 5 - 10 times longer than in eutherians of similar adult body size (Green 1984).

6.3 Evolutionary considerations

Fossil records of the evolutionary development of a behavioral trait such as denning are necessarily scarce. However, denning is believed to have occurred in early Miocene Amphicyonidae carnivores, suggesting a long evolutionary history in the Ursidae and their relatives (Hunt et al. 1983). Denning probably arose in response to food supplies that fluctuated with seasonal environmental changes. Under such conditions it might be more cost-effective for a large well-armed omnivore, with no need to remain lean for either rapid escape from danger or for capture of prey, to deposit fat stores during periods of food abundance and reduce energy expenditures through inactivity and fasting during subsequent periods of food scarcity. The seasonal nature of these fluctuations, however, may have resulted in the period of food abundance being too short to support the full-term development of large, mature neonates, while still allowing these young the time necessary to deposit sufficient fat stores of their own to support winter hibernation. Because of the allometric nature of metabolic processes (Kleiber 1975), ursids, by virtue of their large size, have relatively low energy demands per unit of body weight and therefore require less depression of normal metabolic functions in order to survive a winter's fast than do smaller mammals with proportionately similar fat stores (Morrison 1960, Lindstedt and Boyce 1985). This may have given bears the evolutionary option of supporting developing offspring while fasting, thus allowing them to adopt denning behaviour.

The evolutionary radiation of bears and their relatives has resulted in at least some species living in habitats with sufficient food to allow year round foraging. Polar bears feed primarily on seals on the arctic sea ice through winter, and most do not den for extended periods. However, pregnant females do den in the autumn and, like other ursids, remain without food or water for many months during pregnancy and lactation. At birth the ratio of litter weight to maternal weight is typically low (Kleiman 1983). Giant pandas (*Ailuropoda melanoleuca*) are closely related to modern bears (O'Brien et al. 1985) and also give birth to relatively small neonates, usually single cubs (Kleiman 1983), but unlike temperate and arctic ursids, giant pandas do not spend an extended period in their den after parturition. Instead, the female carries the tiny neonate with her as she forages for bamboo (Schaller et al. 1985). Perhaps because of phylogenetic constraints (Hayssen 1984), female polar bears and giant pandas have not adopted a more typical eutherian gestation length and birth weight, although high-quality food is apparently available to allow foraging before and immediately after parturition.

Physiological constraints on foetal nutrition, as outlined, could have wider ecological implications. For example, when access to carbohydrates is phylogenetically constrained, then shortened gestation, smaller neonates, and a longer period of lactation would be favoured. This may explain why insectivores and carnivores, which subsist on carbohydrate-poor diets, give birth to relatively smaller and less mature neonates than do other orders of mammals (Martin 1984, McKeown et al. 1976). Similarly, different requirements for fats, carbohydrates, and proteins between pregnant and nonpregnant animals could lead to spatial segregation of individuals by reproductive status at times of feeding (e.g., Watson and Staines 1978). Thus, physiological constraints might play as large a role in determining more general trends in neonatal weight as those that have been suggested for mechanical design constraints (Millar 1981), and they may have important consequences for optimal foraging theory.

6.4 Summary

Bears give birth to tiny, immature neonates and display the most extreme deviations from the regression of litter weight on mother weight for eutherian mammals. This may reflect physiological constraints on the ability of a pregnant female to meet the requirements of foetal metabolism while in a state of winter dormancy and without access to food or water. Although all post-natal mammals can use body fat stores to supply energy during fasting, the mammalian foetus does not appear to have the capacity for catabolizing significant quantities of free fatty acids. Instead, it requires glucose as the principle oxidative substrate. However, a fasting female could continue to supply glucose to a developing foetus through gluconeogenesis only by using her body protein, eventually jeopardizing her own survival. By shortening the period of gestation and giving birth to very small, immature neonates, a female would shift from transplacental to mammary nourishment of her offspring. Fatty acids from maternal lipid stores could then be incorporated into milk and used directly for nourishing the offspring, thereby sparing maternal body protein. At the same time, the female would avoid elevated levels of ketone bodies, which might interfere with the maintenance of winter dormancy. The virtual absence of fatty acid catabolism by mammalian foetuses, even in species with an appreciable level of placental transfer of free fatty acids, is in striking contrast to the predominant use of lipids as an energy source by neonates. This notable absence of an energetic pathway in foetuses has never been adequately explained.

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7. LONG DISTANCE ROUTE ORIENTATION OF FEMALE POLAR BEARS IN SPRING[4]

7.1 Introduction

Polar bears (*Ursus maritimus*) are solitary carnivores inhabiting, for at least part of each year, the pack ice of arctic and subarctic waters (review in DeMaster and Stirling 1981). Data obtained from mark/recapture studies and returns of tags from bears killed by Inuit hunters indicate that the world population of polar bears is broken into a series of semi-discrete sub-populations. Consistent with the idea of discrete subpopulations, tagged polar bears have shown relatively marked seasonal fidelity to their region of capture, although in intervening seasons they may move considerable distances (Larsen 1971, Lentfer 1972, Schweinsburg et al. 1982).

Unlike terrestrial Ursidae, polar bears appear not to defend discrete territories. An individual polar bear may usurp a prey item from another bear (Stirling 1974), but there are no data to suggest the defense of a defined space (Hansson and Thomassen 1983, Latour 1981). Given the labile nature of the sea ice habitat, the defense of territories there is unlikely to be energetically cost-effective. Consequently, individual bears may move linear distances of several hundreds of km annually in search of suitable hunting sites, mates, and maternity den sites.

Throughout the Arctic there are localized regions on land where relatively large numbers of pregnant females enter dens and hibernate over winter (Harington 1968, Larsen 1976, Uspenski and Kistchinski 1972). Such a region is found in northeastern Manitoba, Canada on the west side of Hudson Bay (Jonkel et al. 1972). These regions are traditional denning areas and are used by adult females each year. Pregnant females enter individual hibernacula alone in autumn and cubs are born in an altricial state during midwinter (Lønø 1970). Adult females and their newborn cubs-of-the-year remain in their hibernacula until early spring and emerge between late February and April, depending on the population. After several days spent in the immediate vicinity of the vacated hibernacula, the families move off to the sea ice (Hansson and Thomassen 1983).

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On Hudson Bay all the sea ice melts each year forcing all polar bears ashore in summer (Stirling et al. 1977). Adult females, cubs, and juvenile bears move inland soon after arriving ashore, while adult males tend to remain along the coast. In autumn, the bay refreezes and all bears, except pregnant females, return to the sea ice. Wintering females return to the sea ice the following spring when the ground is snow-covered and thereby make readily identifiable tracks of their passage. This afforded us the opportunity to determine the exact routes taken by bears leaving the denning region at that time.

Kolenosky and Prevett (1983) reported on the direction of spring movements made by polar bear family groups as they moved from inland maternity den sites in Ontario, Canada to the Hudson and James Bay coastlines. Routes followed tended to be perpendicular to the coast and essentially straight. Although the actual headings of tracks were not given, Kolenosky and Prevett (1983) concluded that the ability of the adult females to follow constant headings was "remarkable" and indicated a well developed navigational sense. Similar directional movements of polar bears from inland denning regions adjacent to Hudson Bay were suggested by Jonkel et al. (1972). However, to date no specific data have been published that demonstrate oriented and directed movement of polar bears. In this paper I assess the degree of orientation of movements of female polar bears travelling from winter den sites to the sea ice in spring.

7.2 Methods

Studies were conducted in the Hudson Bay lowlands of NE Manitoba, Canada to the south and east of the town of Churchill. This region lies at the boreal forest - tundra ecotone and is characterized by long cold winters and short cool summers. Each fall pregnant female polar bears enter dens in this region, approximately 20-100 km inland from Hudson Bay (Jonkel et al. 1972). Each spring approximately 80 - 100 adult female bears with their accompanying newborn cubs-of-the-year and a smaller number of adult females without accompanying cubs emerge from their winter dens and walk to the sea ice of Hudson Bay. As part of an ongoing investigation into polar bear reproductive ecology, we surveyed for and captured bears during March 8 - 19, 1980; Feb. 26 - March 25, 1981; February 13 - March 29, 1982; March 2 - 23, 1983; and February 29 - March 24, 1984.

A Bell 206B JetRanger helicopter was used for all searches, flying at altitudes ranging between 5m and 150m above ground level and at ground speeds between approximately 10 and 200 km/hr. Generally flights followed along river courses and around the margin of lakes with banks suitable for denning. When tracks of polar bears were detected they were followed until the bears were located or the tracks were lost. On some occasions tracks were also back tracked to a maternity den. In both cases the routes taken were plotted on 1:250,000 topographic maps (National Topographical Survey of Canada, Ottawa). Tracks made by family groups were considered separately from tracks made by solitary bears and only those tracks that could be followed for more than five km were included in analyses. I was not able to determine the identity of a bear that had made a particular track unless it was sighted or captured along that track. Consequently, I treated each track followed in a single year as independent from each other track followed that same year.

When sighted, adult bears were captured using rifle-fired darts, each containing ketamine hydrochloride and xylazine hydrochloride, administered from the helicopter (Lee et al. 1981). Each bear was assigned a permanent identifying number, had a premolar tooth extracted for aging purposes, and had a temporary number dyed on its back to facilitate subsequent identification from the air (Stirling et al. 1977). Extracted teeth were decalcified, sectioned on a cryostat, mounted on microscope slides, and stained with toluene blue. Ages were determined from counts of cementum annuli (Grue and Jensen 1979).

Statistical analysis of movement data was carried out in two stages. A mean heading was determined for each track by subdividing the plotted route into 2.5 km vectors, determining the heading for each vector, and then summing the vector components in a first-order analysis to give a mean track heading and an overall mean vector length. To determine the collective mean heading of all family groups or all solitary bears, the individual mean headings were summed using second-order statistical analysis for directional data (Batschelet 1981). Second-order analyses of directional data require that the first-order analysis for each track be based on the same number of observations for each individual. I could not control how far individual tracks tracks could be followed and, consequently, the data do not meet this requirement. However, as the mean length of tracks followed, the range of lengths of tracks, and the number of tracks followed was similar for all five years of the study I accepted that the requirement of equal numbers of observations per individual was approximately met. The resultant second-order vectors of the overall mean headings for family groups and for solitary bears were used as test statistics for Moore's nonparametric bivariate modification of the Rayleigh test for directionality (Batschelet 1981).

The median age of females with cubs-of-the-year was compared with the median age of solitary females using the Mann-Whitney U-test at a significance level of 0.05 for a two-tailed test (Conover 1980).

7.3 Results

The ability to follow tracks varied with weather conditions. Tracks were most visible on calm sunny days, immediately following a fresh snowfall, when there was little or no wind to cause drifting and when direct sunlight created shadows thus highlighting relief in the snow. There was no difficulty distinguishing tracks made by polar bears from those of the only other large terrestrial mammals in the study area during spring: caribou (*Rangifer tarandus*), moose (*Alces alces*), and wolves (*Canis lupus*).

We followed 1081 km of polar bear tracks and handled 119 adult female bears. Thirty-three of these bears were captured after being tracked while the remaining 86 were either captured at den sites or after being tracked for fewer than 5 km. No males other than cubs-of-the-year were handled within the Manitoba inland denning region in spring. Consequently all tracks of solitary bears followed (n = 10) were assumed to have been made by adult females. No evidence was gathered to suggest that behaviour of travelling bears was affected by the helicopter, at least prior to close approach for drug immobilization. The heading and rate of travel of bears did not vary as the helicopter approached during tracking. Bears resighted or tracked after handling did not show aberrant headings nor rates of travel.

7.3.1 Family groups

Sixty-four family groups were tracked for 929 km over the five years of the study (Table 7-1). Their routes followed a relatively constant heading, both within and between years (Fig. 7-1a to 7-1e). A striking feature of the family group tracks were their linear nature over intervals of 5 km or longer. Course alterations were made infrequently, usually no more than one or two over the length of track followed.

There was no evidence that females changed headings specifically to locate food items along their course of travel. At infrequent intervals along a track one or two shallow pits would be dug in the snow, presumably places where the bears rested and cubs were nursed during travel. At these resting sites the adult bears would occasionally dig through the snow and feed on sedges (*Carex* spp.). No other evidence of feeding by adult females while travelling to the sea ice was observed.

The only times family group tracks varied from straight headings were when they were found in association with wolf tracks (Ramsay and Stirling 1984). On those occasions the family group tracks followed highly convoluted routes with no apparent general heading. Presumably the behaviour of the bears was influenced by the presence of wolves and the non-oriented tracks reflected avoidance movements on the part of the bears. In all cases where snow conditions allowed tracking of families, following association with wolf tracks, their tracks took a generally northeasterly heading ($n = 4$). Tracks found in association with wolf tracks were excluded from the data reported here.

Although over-winter dens were invariably found along lakeshores and streambanks, tracks of travelling bears rarely followed river courses for more than two or three km. Instead they generally passed over windswept tundra and only crossed rivers en route (Fig. 7-1).

The headings of families tracked were significantly non-random for all years pooled ($D = 3.87$, $P < 0.001$, Moore's nonparametric test) with an overall mean heading of 39.4° and a marked clumping of individual headings in the northeastern quadrat (Fig. 7-2a).

Only one adult female with accompanying cubs-of-the-year was captured on two separate years while travelling from the denning region in spring (Fig. 7-1b, 7-1d). The portion of her route tracked was similar in location and heading in both years (1981 - 26.3° ; 1983 - 31.9°).

Track patterns indicate that when family groups reached the sea-ice their activity behaviour changed. Instead of moving with a relatively constant heading, the bears began following lead systems and ice pressure ridges. It appeared that bears began hunting seals soon after they reached suitable habitat (Stirling 1974). As my research design precluded following most groups once they reached the ocean, I have few data concerning their offshore movements on Hudson Bay.

7.3.2 Solitary bears

Solitary bears or their tracks were seen in each year of the current study. Nine solitary bears were handled in spring in Manitoba over the five years of the current study, including two females captured at their winter den, each with a single dead cub of the year.

Tracks of solitary bears took a wider range of headings than did those of family groups (Fig. 7-1f). Tracks of solitary bears were also more circuitous than those of family groups. Whereas the tracks of individual family groups showed little change in direction of heading over distances of five km or more, travelling solitary bears frequently changed direction every 200 - 300 m.

While travelling, solitary bears differed in other behaviour from females with accompanying cubs-of-the-year. Solitary bears frequently excavated snow caves of one or more metres depth along their routes of travel. For example, one solitary bear travelled more than 14 km during a 16 hour period, dug three snow caves and numerous shallow pits, and followed a highly convoluted route, often changing heading every 50 m. By contrast, females with accompanying cubs-of-the-year were never observed to have dug snow caves nor multiple clusters of pits along their routes to the sea ice.

The overall mean heading taken by solitary bears of 27.2° was found to be significantly oriented for all years pooled (D = 1.14, $0.01 < P < 0.05$, Moore's nonparametric test). However the clumping of headings in the northeastern quadrat is considerably less marked than for family groups (Fig. 7-2b). Thus, it appeared that although solitary bears followed, on average, a heading similar to females with cubs, they do so with greater angular variance. One solitary bear followed a relatively direct heading of 281° over the distance tracked. Such a heading would not lead to the sea ice of Hudson Bay.

Whereas the median age of females with accompanying cubs-of-the-year handled in Manitoba in spring was 14.7 years (n = 119) the median age of solitary females in spring was 21.0 years (n = 9), a difference which is significant (U = 322.5, P = 0.04).

7.4 Discussion

The region of polar bear denning in northeastern Manitoba is located approximately 20-100 km inland from the sea. The mothers winter in a maternity den without access to food from the time of den entrance to the time of emergence. In spring accompanying cubs sustain themselves entirely by nursing. Other than sparse vegetation and carrion found under snow on land, the only available food for the mothers are seals in Hudson Bay. Since family groups, leaving the region in spring, must make an extensive overland trek, it is not surprising that they follow a direct and oriented route to the sea. If they are to reach the sea ice from the denning region of Manitoba they must take a mean heading of between approximately 320° and 130°, in a clockwise direction. Because the coastline east of the denning region runs approximately north-south, the shortest route to the ocean for most bears inland would be along a heading of approximately 80°. The constancy of headings of families clustered about 39° in all years was unexpected. Clearly, the bears did not follow random routes within the range of headings that would allow them to reach the ocean nor did they follow the geometrically shortest route to the sea ice.

Kolenosky and Prevett (1983) described similar oriented movements of polar bears in Ontario although they did not report the mean headings taken by individual families. Those families of polar bears from dens near James Bay also did not take routes directly toward that closest body of water but instead took a more northerly heading to Hudson Bay. However, as most polar bears in Ontario are not found near James Bay and as the

Hudson Bay coastline of Ontario runs generally east-west, most of the routes reported by Kolenosky and Prevett (1983) do take the shortest route to the sea ice.

From 1970 - 1976 the Wildlife Branch of the Department of Natural Resources, Government of Manitoba flew fixed-wing aerial surveys to count polar bear family groups in the study area during spring (unpublished reports). Because tracks could not be readily followed by fixed-wing aircraft, these data are not directly comparable with those reported here. None the less, 93% (*n* = 114) of the tracks recorded had headings of between 20° and 50°, similar to the mean of 39.4° reported in this study.

Female bears in our study population first produce cubs at about five years of age with subsequent litters being produced every two or three years (Ramsay and Stirling 1982). Because all bears are forced ashore each year and as juvenile bears move inland, primiparous females would thus have travelled to the vicinity of their respective natal region each summer in the years prior to their first pregnancy. These would include trips with their mothers prior to weaning and solitary trips in years following weaning. Each autumn the young bears would return to the sea ice from their inland summering site. Such forays might allow sufficient familiarity with the region to enable a primiparous mother to orient in spring by landmark recognition alone. Whether regional familiarity is sufficient to account for the oriented movements observed and what the actual cues are that might be used by the bears is not known. In spring, prevailing winds are most commonly from the northwest at approximately 90° to the mean heading taken by the families (Environment Canada data for Churchill, Manitoba). Major watercourses in the denning region are tree-lined and tend to flow eastward but did not appear to be used by the bears as sheltered routes to Hudson Bay.

Small numbers of solitary bears or their tracks were reported in spring in northeastern Manitoba by Jonkel et al. (1972), Stirling et al. (1977), and in an adjacent region of Ontario by Kolenosky and Prevett (1983), similar to the pattern observed in this study. I have assumed that the solitary bears followed were females that had probably been pregnant and had lost their litters. As many of the solitary females tracked or handled in the Manitoba denning region in spring were relatively old they might have included a high proportion of bears that had reached reproductive senescence and could not successfully produce a litter. In spring such bears might have experienced an endocrine balance appropriate for a female nursing and caring for newborn cubs but without the cubs to provide necessary feedback cues. An inappropriate suite of behaviours might therefore have been displayed after emergence from the maternity den. Because solitary females are not nursing cubs their energy expenditures should be less than those of a nursing female. Therefore solitary females might not have as great a need to return to active hunting and feeding as do actively lactating females. The rather more circuitous routes followed by solitary bears, coupled with evidence of their pit digging behaviour while travelling, suggests they are less highly motivated than females with cubs-of-the-year to return to the sea ice.

Stirling et al. (1977) suggested there may be a concentration of bears on the sea ice in spring to the northeast of Cape Churchill, probably associated with an offshore lead system there. The constant heading taken by family groups leaving the Manitoba denning region would tend to take them toward that lead system. Animals moving to a discrete locale from scattered origins might be expected to show convergent paths. Instead the tracks observed tended to follow parallel courses. However, if the location of the lead system varies from year to year then the bears may do better energetically to take a general heading to the expected lead vicinity rather than to take a precise heading to an imprecisely known location. A relatively consistent northeasterly heading for bears in Manitoba may represent an optimization of route, allowing a family group to, on average, arrive at the sea coast relatively close to a region of active sea ice and, very likely, associated good hunting. As noted by Jonkel et al. (1972) and Kolenosky and Prevett (1983), family groups to the south and east of our study location tend to move directly north, essentially perpendicular to the coastline. Such headings would follow the shortest distances to potentially productive areas for seal hunting in that region of Hudson Bay. As capture operations for polar bears were not conducted in Ontario, I do not know if there is any interchange between females from our study population and from those areas. Hence no data are available to determine whether individual females vary the headings of their post-denning movements depending upon the location of their winter den.

In Manitoba, when polar bears come ashore from the melting ice in August, females and family groups move inland to the denning region. At present there are few data concerning the routes taken by these bears nor do I know the routes taken by the family groups and juveniles, in fall, as they return to the coast to rendezvous with the newly formed ice. It would be of interest to know whether bears returning to the Manitoba denning region in summer follow direct headings.

I have demonstrated that polar bear family groups can orient along a relatively precise heading when leaving a denning region. Bears possessing such a skill may also be able to use it to move to seasonally productive hunting regions or to return to natal areas for maternity denning. For animals living in a temporally variable environment with resources distributed in a widely scattered patchy arrangement, the ability to orient spatial movements would appear to be highly adaptive.

7.5 Summary

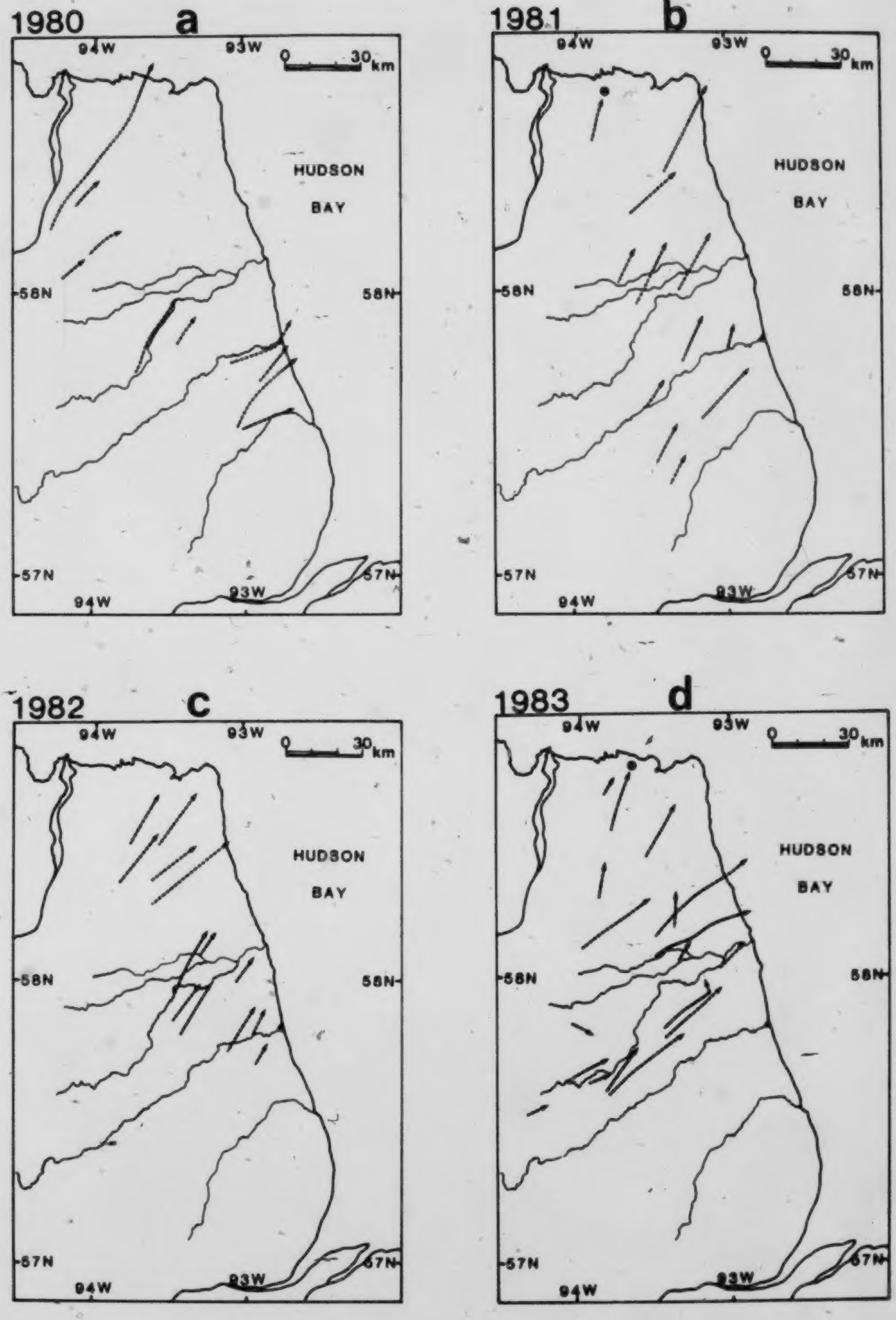
Adult female polar bears in northeastern Manitoba, Canada were followed, using tracks left in snow, as they moved from the region of their winter dens to the sea ice of Hudson Bay in February and March.

Mothers with accompanying cubs-of-the-year travelled along relatively straight independent routes with a mean heading of approximately 39°. Tracks did not follow obvious physiographic features of the landscape, nor did they follow the shortest routes to the sea ice.

Tracks of solitary bears were assumed to be made by adult females that had lost litters as no adult males or sub-adult polar bears have ever been captured in the Manitoba denning region in spring. Although the mean heading taken by solitary bears was similar to that taken by family groups, their routes were much more convoluted. Solitary bears also displayed more snow digging activity and seemingly aimless wandering.

Figure 7-1a to 7-1e. Maps of study area showing routes taken by polar bear family groups tracked in February and March, 1980 - 1984. Tracks marked with ● were made by the same adult female in 1981 and 1983.

Figure 7-1f. Map of study area showing routes taken by solitary polar bears tracked during February and March, 1980 - 1983.


1980
a
94W
93W
0
30 km
HUDSON
BAY
58N
57N
1981
b
1982
c
1983
d

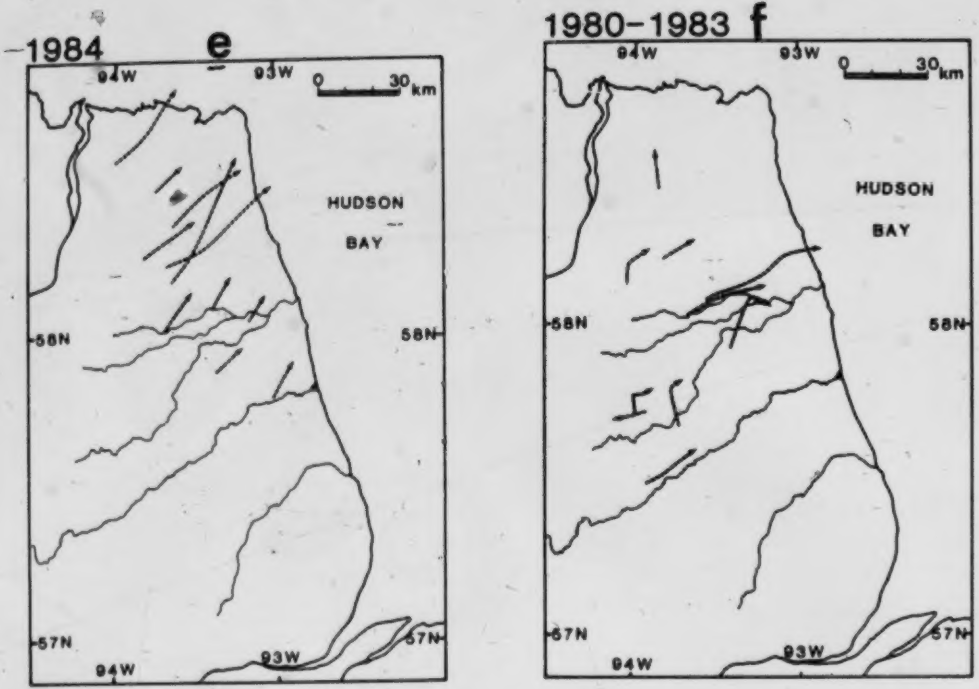
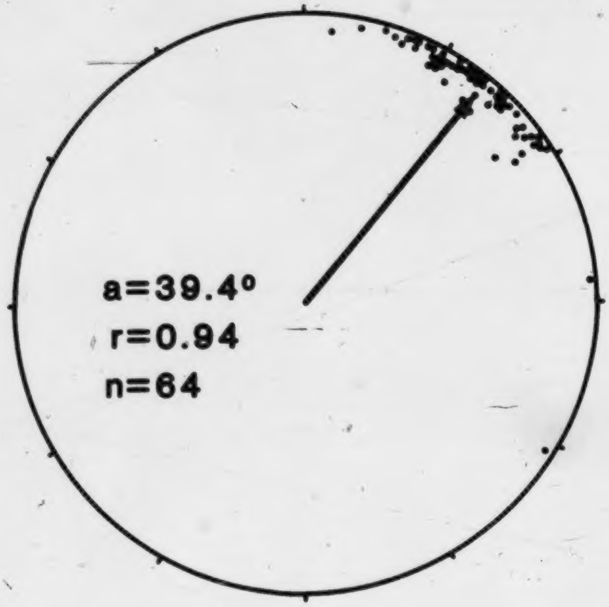

1984
e
94W
93W
0
30
km
HUDSON
BAY
58N
58N
57N
57N
94W
93W
1980-1983
f
94W
93W
0
30
km
HUDSON
BAY
58N
58N
57N
57N
94W
93W

Figure 7-2a. Orientation of tracks of polar bear family groups leaving the Manitoba denning region, February and March, 1980-1984.

Figure 7-2b. Orientation of tracks of solitary polar bears leaving the Manitoba denning region during February and March, 1980 - 1983.

True north is to the top of figures: a = mean heading of composite vector; r = length of the composite vector on the unit circle, a measure of variance; *n* = sample size. (●) represent mean direction and variance of each track from first-order analysis.

a



b

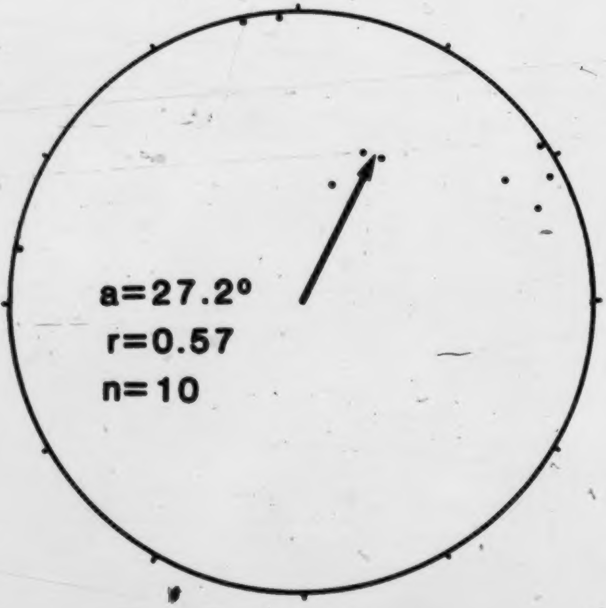


Table 7-1. Movement data of adult female polar bear tracks followed in northeastern Manitoba in February and March (1980-1984).

Reproductive status	Year	No. tracks followed	Total distance tracked (km)	Mean distance tracked (km)	Mean heading of tracks (a)	Mean vector length (r)
with cubs	1980	10	148	14.8	46.5°	0.92
with cubs	1981	12	185	15.4	34.7°	0.97
with cubs	1982	13	168	12.9	35.9°	0.97
with cubs	1983	18	260	14.4	42.0°	0.88
with cubs	1984	11	168	15.3	38.3°	0.97
with cubs	1980-84	64	929	14.5	39.4°	0.94
Alone	1980-83	10	152	15.2	27.2°	0.57

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8. SUMMARY

Bears display a number of characteristics associated with their reproductive biology that are rare or uncommon among eutherian mammals. These include delayed implantation, gestation and early lactation during maternal fasting, anomalously small birth size, a long lactation period, and a relatively low fertility ratio. These characteristics intrigued me and I have attempted to understand their ecological implications and adaptive significance.

I have described basic reproductive parameters from a population of polar bears inhabiting western Hudson Bay, near the southernmost extent of their circumpolar range. Where possible, I have made comparisons with data collected from more northerly populations. The bears of western Hudson Bay have a higher natality rate and a shorter interbirth interval than those from any other polar bear population studied. Yet their growth and mortality rates are little different from those other populations. I have speculated about causes for some of these similarities and differences and have suggested initial tests for the hypotheses proposed.

I collected only limited data on age-specific mortality rates in polar bears and little more is known from any other population. I did not collect any information on the extent to which juvenile growth rates affect subsequent survival. If such data were available, it might then be possible to interpret age-specific reproductive tactics of polar bears (Pianka and Parker 1975). These data are not easy to generate, however, and require a long-term commitment to ongoing field studies. The benefits that might accrue from studies of this nature include increased insight into the proximate and ultimate causes of reproductive life-history traits as well as the development of predictive models of reproductive strategies.

The labile nature of sea ice does not allow polar bears to establish territories or permenant home ranges. This constraint has resulted in the evolution of a mating system qualitatively different from that of other species of bears and that of most terrestrial carnivores. I have presented a first description of some aspects of the polar bear mating system, have speculated on some of the resulting ecological implications, and have proposed questions that may be fruitful for further study.

Temporal and spatial variability in resource availability throughout the Arctic may have resulted in selection for animals that could accommodate unpredictable periods of acute food shortages, and hence obligatory fasting, at somewhat unpredictable intervals. I present preliminary data that is consistent with the model that polar bears can enter a metabolic state similar to that of a hibernating black bear, but while active and at any season rather than just in late autumn. Controlled feeding experiments are the next step necessary to verify this hypothesis and determine whether the ability to shift metabolic states is as facultative as proposed.

Speculation on the anomalously small size of bear cubs at birth resulted in a physiological model that proposes that females are constrained from maintaining pregnancy while fasting. The model also notes the apparent functional absence of fat catabolism by foetuses of any mammalian species, a striking exception as fat catabolic pathways are frequently, often exclusively, used by neonates for meeting their energy needs. This model may have even wider applicability in understanding other life-history phenomena in both birds and mammals including size of brains at birth and the evolution of viviparity.

An ability to locate required resources is necessary for life in a heterogeneous environment. I was able to demonstrate the ability of adult female polar bears to travel in a directed fashion for moderately long distances. Determining the underlying control mechanisms for navigational skills and the frequency of their expression remains for future studies. The marked differences between sea ice and the terrestrial habitats where most mammalian navigation research has been conducted may offer opportunities for fruitful comparative studies. Because of the presence of the north magnetic pole in the Canadian Arctic and the labile nature of sea ice, some cues used for navigation by terrestrial species, such as the detection of magnetic fields and familiarity with landmarks, may be of less value to polar bears throughout much of their range.

Like much research, my work suggests more questions than it answers. I have no conceit that I have produced the definitive work on the biology of reproduction of polar bears. A five year study of a single population of a species in which females are sexually immature until five years of age and have an interbirth interval of two years has obvious limitations. For a long-lived animal, nothing short of a determined, difficult, and expensive long-term study could hope to approach full understanding. It would be productive to follow one or more cohorts through their complete lifespan, in order to determine individual lifetime success and to see how reproductive parameters vary with changing environmental conditions. Whether such a study is practical remains to be seen. Instead, I have attempted to offer, in broad brush strokes as it were, an outline of the topic.

My research suggests three major areas for further investigation. A common theme running through Chapters 3 to 7 is that the spatial and temporal distribution of food resources influences the behaviour, physiology, and population dynamics of polar bears. Understanding their access to food resources is, in many ways, the key to understanding the ecology of polar bears. Since the primary prey of polar bears are seals, further studies of the inter-relationship of polar bears with the various species of seal prey are desirable. Data are especially needed from late spring and early summer when polar bears appear to realize their maximum annual growth rates as well as attain their greatest body weight. Polar bears experience a pronounced "boom-and-bust" annual feeding cycle that probably influences the reproductive performance of females in any year. Data are needed on the degree of interannual variability of body reserves and their relationship with variability in reproductive performance. Currently, body weight is the best predictor of physical condition in bears. A more refined approach, perhaps measuring body composition directly, is desirable.

A second major topic suggested for future research is the description and measurement of unpredictability in the Arctic environment relative to its effect on polar bears. An understanding of how environmental change relates to the biology of reproduction in any mammal is needed as is a predictive theory of how such change would manifest itself in other life-history phenomena. To some extent, unpredictability of the environment, over both short and intermediate time frames, appears to be commonly experienced by many animals (Weatherhead 1986). The Arctic experiences greater climatic unpredictability than many temperate or tropical regions, probably because of the absence of buffering capacity in its relatively simple ecosystem. Understanding environmental unpredictability is difficult because it is not clear what the relevant variables are. Smith and Stirling (1978) and Picton (1978) have made initial attempts at such an investigation for polar and brown bears respectively, but the field has scarcely been touched. The relatively large-scale climatic fluctuations occurring in the Arctic and the relatively simple predator-prey relationship of polar bears and seals suggest that this may make an ideal system for study, assuming that logistic difficulties can be overcome.

A third major field of future investigation is in the field of health sciences. Polar bears may be excellent subjects for comparative physiological studies and in human medical research. Their apparent ability to fast facultatively while sparing body protein warrents further study which may result in the development of important heuristic models of metabolism during fasting. An understanding of polar bear intermediate metabolism might lead to the development of new treatments to help patients with kidney disease reduce their dependence on dialysis therapy. Greater understanding of the metabolic changes that occur during the large annual weight changes of polar bears might shed light on questions relating to human obesity, body weight set points, and the long term effects of dieting (Mrosovsky and Sherry 1980).

The ancestors of polar bears who first ventured out onto a frozen sea to hunt seals brought with them a splendid array of preadaptations for life in an environment fundamentally different from the one they had left. Bears are mammals quintessentially adapted to cope with unpredictability on time scales of months and years. Clearly, abundant nutrient stores, primarily fat, must be accrued by a mammal prior to undertaking an extended fast. However, there are physical and ecological constraints on the amount of adipose tissue that can be stored *in vivo* (Pond 1978). The large body size of bears offered allometric advantages, both when fasting and when accruing body reserves, and offered a favourable volume-to-surface-area ratio for life in a cold environment (Morrison 1960, Boyce 1979, Kingsley et al. 1983, Calder 1984, Lindstedt and Boyce 1985). Large body size allowed the killing of the relatively large prey species found in the Arctic as well as the means for gaining access to seals under snow and ice cover. Further, except for humans and occasionally conspecifics, polar bears have no predators and thus need not remain lean for rapid escape from danger. Similarly, bears rarely capture prey by cursorial pursuit. Thus, polar bears, the most carnivorous of bears, rely predominantly on still-hunting and stalking prey (Stirling 1974). As large, well-armed mammals, bears occupy a niche in which acquisition of considerable fat stores would have little effect on either hunting success or predator avoidance. Their metabolic adaptations for extended fasting during hibernation were modified to allow fasting at any season, not just during winter. Extended mother-cub associations offered environmental buffering for young bears and allowed them greater opportunity to achieve a larger body size and perhaps a more extensive behavioural repertoire before independence, traits that might confer survival advantages in an unpredictable environment. Low adult mortality rates allowed long-term iteroparity and the option of abandoning current reproductive effort in poor years and waiting until conditions improved for a later breeding attempt. Although modified, these ursid characteristics have allowed polar bears to achieve the greatest distribution on the circumpolar arctic sea ice of any terrestrial mammal.

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